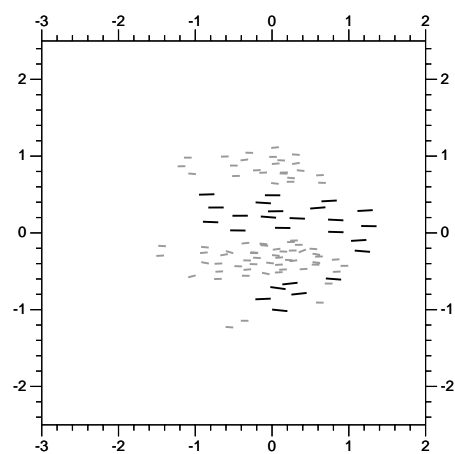
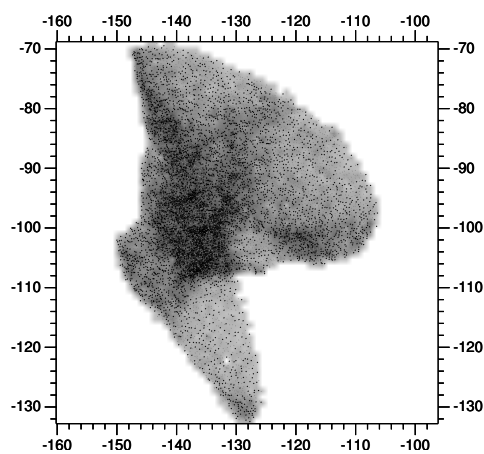


Implications of Embodiment and Situatedness on the Social Organization of Fish Schools

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Implications of Embodiment and Situatenedness on the Social Organization of Fish Schools

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The Faculty of Economics, Business Administration and Information Technology of the University of Zurich herewith permits the publication of the aforementioned dissertation without expressing any opinion on the views contained therein.

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Abstract

In this thesis we investigate how the social organization of fish schools is influenced by the morphology and the sensory capabilities of the individuals as well as by those of their predators. We do this by means of individual-based models. Here, behavior at the group-level (schooling) is a consequence of local interactions, i.e. the responses of individuals to their neighbors and the interactions between predator and prey. We demonstrate how modeling the embodiment and the perceptual capabilities (situatedness) both of the individuals and of the predator influences their interaction and therefore the patterns at the group-level.

Representing the individuals' body affects the inter-individual spacing, such that large individuals occupy more space compared to small ones. Modeling the individuals' situatedness, by reflecting the masking of distant neighbors by closer ones, restricts interaction to the local environment of the individual. This influences many schooling characteristics, such as nearest neighbor distance or group speed, and in mixed schools of large and small individuals it leads to the segregation of the two sizes. In large groups school shape becomes complex and variable and the distribution of individuals heterogeneous, with regions of high and low density occurring anywhere in the school.

Modeling morphological and sensory constraints of a predator affects its success in capturing prey and, therefore, influences whether schooling behavior is beneficial for the individuals or not. We demonstrate that when the predator is confusable, i.e. when its sensory capabilities to detect the movements of individuals in a group are limited, schooling is almost always beneficial.

In summary, incorporating aspects of embodiment and situatedness leads to more realistic models, first, because the real world is reflected more accurately, and, second, because they lead to a more realistic social organization of the simulated schools.

Zusammenfassung

Diese Dissertation beschäftigt sich mit der Frage, wie die soziale Organisation von Fischschwärmen von der Morphologie und der sensorischen Wahrnehmung der Fische abhängt. Wir betrachten dabei sowohl die Fische, die den Schwarm bilden, als auch die Raubfische, die den Schwarm attackieren. Das Verhalten auf Gruppenebene, also das Schwarmverhalten, ist eine Folge der lokalen Interaktionen, der Reaktionen der Fische auf ihre Nachbarn. Wir zeigen, dass sowohl die Modellierung des Körpers (embodiment) als auch der sensorischen Wahrnehmung (situatedness) der Fische sowie der Räuber diese Interaktionen beeinflusst und darum auch zu veränderten Mustern im Gruppenverhalten führt.

Wird der Körper der Fische in einer Schwarmsimulation miteinbezogen, beeinflusst dies die Abstände zwischen den Nachbarn, da dann grosse Individuen mehr Platz beanspruchen als kleine. Wird die sensorische Wahrnehmung modelliert, indem berücksichtigt wird dass ein Teil der Nachbarn hinter solchen die sich näher befinden verborgen und somit unsichtbar sind, interagieren nur noch unmittelbare Nachbarn. Dies beeinflusst viele Eigenschaften des Schwarmverhaltens, unter anderem die Distanz zwischen nächsten Nachbarn oder die Schwimgeschwindigkeit des Schwarms. In gemischten Schwärmen, bestehend aus grossen und kleinen Individuen, gruppieren sich dann grosse Individuen bevorzugt mit grossen Nachbarn und kleine Individuen entsprechend mit kleinen. In grossen Schwärmen mit vielen Individuen wird die Form des Schwarms sowie die Anordnung der Individuen unregelmässig und ändert sich auch im Laufe der Zeit. Es bilden sich z.B. Einbuchtungen und Ausstülpungen, während gleichzeitig die Dichte der Fische an einem Ort im Schwarm zu- und an einem anderen abnimmt, wie man dies auch in der Natur beobachtet.

Modelliert man die morphologischen und sensorischen Einschränkungen des Raubfisches, so beeinflusst dies seinen Jagderfolg, und bestimmt somit auch, ob sich Schwarmverhalten für die Fische lohnt oder nicht. Wir zeigen insbesondere dass Schwarmverhalten in den meisten Fällen vorteilhaft ist, wenn der Raubfisch von der Masse der Beutefische “verwirrt” wird.

Zusammenfassend können wir sagen, dass die Miteinbeziehung von Körper und sensorischer Wahrnehmung zu realistischeren Modellen führt. Einerseits weil solche Modelle die Situation in der realen Welt genauer abbilden, andererseits weil sie auch zu natürlicheren Mustern in der sozialen Organisation der simulierten Fischschwärme führt.

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Chapter 1

Introduction

Almost all living organisms, from bacteria to higher vertebrates, aggregate with con-specifics for longer or shorter periods of time. Such aggregations are often associated with striking patterns, for example the dendritic structures of bacterial growth (Fig. 1.1), the living bridges built by army ants (Fig. 1.2) or the diverse maneuvers displayed by schools of fish (Figs. 1.3-1.5). Common to these examples is their astonishing structural order. Sometimes, individuals are coupled so tightly that they seem to behave as a single organism. Naturally, such phenomena attract a lot of interest and raised two general questions: *why* and *how* the animals are doing it.

In some cases, it seems clear how such aggregations come about. In the case of the bacteria, the tree-like structures form because of the interaction between bacterial growth and the availability of nutrients in their environment, suggesting that there is no purpose or function associated with the pattern (e.g. Ben-Jacob et al. 1994).

In the case of the army-ant bridges, the function is obvious – the ants build bridges to cross gaps –, whereas the mechanism, how the ants coordinate themselves in order to build it, it not well understood (e.g. Anderson 2002). The difficulty is that we can only observe the behavior at the group level, from which is difficult to draw conclusions back to the actions of the individuals.

This is even more true for schools of fish and flocks of birds because they form very large groups, in the case of herring comprising up to several million individuals. Even in such large aggregations the coordination of movements is remarkable. Astonishingly, the individuals achieve this by simply adjusting their movements to those of their close by neighbors, without a need for a leader or external cues, as suggested by biological evidence (Parrish and Viscido 2005).

Such a system, where there is no global control is called *self-organized*. The behavior at the group-level (schooling) is a consequence of the actions at the individual-level. Thus, schooling is *emergent* from the *local interactions* between the individuals.

In this thesis, we investigate such emergence of schooling behavior of fish by means of *individual-based models*.

Individual-based models focus on the actions of and interactions between the individuals and are used to investigate how the behavior at the group-level emerges from the actions at the individual-level. Such models, therefore, can elucidate the question *how* fish school. By combining an individual-based approach with *evolutionary algorithms*, however, it is also possible to investigate the conditions under which schooling behavior is advantageous, shifting the focus on the question *why* fish school.

The work described here is the result of combining such individual-based modeling with



Figure 1.1 – Fractal dendrites formed by bacterial growth. Reprinted with the kind permission of Eshel Ben-Jacob.

ideas originating from *embodied artificial intelligence*. Embodied artificial intelligence states that intelligent behavior is the result of an agent's *interaction with its environment* (Pfeifer and Scheier 1999), assuming that an intelligent agent must be *embodied* (represented by a physical body) and *situated* (extracting information on its environment by its own sensors). In contrast to classical artificial intelligence, which focuses on control algorithms, the behavior of an embodied agent depends both on its 'brain' (the control algorithm) as well as on its morphology.

The concepts of embodiment and situatedness were developed originally for building physical robots acting in the real world. But they fit seamlessly into the individual-based simulation approach. Both, embodied artificial intelligence and the individual-based approach, emphasize that behavior is generated by the individuals' interaction with its environment, which in the case of individual-based models are the other individuals. Furthermore, by concentrating on local interactions, individual-based models of self-organized systems have an element of situatedness already present by design.

In contrast to the real world, where situatedness and embodiment are given, in simulation models their inclusion is a matter of degree. More or fewer characteristics of the morphology (and the physical properties of the environment) can be incorporated into the simulation.

In the present thesis, we demonstrate that including elements of embodiment and situatedness in individual-based simulations leads to more realistic models, because they reflect the real world more accurately. Furthermore, we find that their inclusion also leads to more realistic social organization of schools and are necessary in evolutionary models to explain benefits of schooling behavior.



Figure 1.2 – A “living bridge” built by army ants (Eciton burcellii). Photo by: Alex Wild.

1.1 Self-organized systems and emergence

Self-organization, a concept originally developed to understand physical systems (dynamical systems theory, e.g. Ashby 1947; Nicolis and Prigogine 1977), is nowadays applied throughout science. It is important to understand many biological phenomena (e.g. Camazine et al. 2001) such as morphogenesis, homeostasis, and also collective phenomena such as structures created by social insects and the dynamic properties of flocks of birds and schools of fish.

Self-organization is the process, by which *structure* or *order* appears in a system without a central or external mechanism imposing it. Instead, the global patterns result from the *interactions* between the constituting parts of the system. In other words, the patterns observed at the global level *emerge* from the interactions at the local level (see e.g. De Wolf and Holvoet 2005). Interestingly, complex behavior at the global level can often be explained by surprisingly simple local rules (Langton 1995).

Examples of self-organizing systems are: Rayleigh-Bénard convection cells (Getling 1998) in physics, the Belousov-Zhabotinsky reaction (Zhabotinsky 1964) in chemistry, or in biology the aggregation behaviors found in many species of animals (for an overview see Camazine et al. 2001; Hemelrijk 2002a).



Figure 1.3 – A school of bluestripe snapper (*Lutjanus kasmira*). Photo by: Jim and Becca Wicks.

1.2 Individual-based models

Mathematical models of self-organized systems in general and of aggregating animals in particular can be classified into two categories, Eulerian and Lagrangian models.

Eulerian models use partial differential equations to describe the flux of a property (how that property changes spatially and temporally). In the case of aggregating animals this property is the population density. While using partial differential equations for modeling has certainly its merits due to the mathematical tools available, this approach has the disadvantage, that it does not allow to trace the properties at the group-level back to the behavior of the individuals (DeAngelis and Mooij 2005) and many biologically relevant features, such as perceptual limitations and individual variations (e.g. in body size), cannot be incorporated into such models (Gautrais, Jost, and Theraulaz 2008).

In Lagrangian models, aggregation behavior is modeled at the individual level, by specifying the equation of motion of the animals. For this reason, they are often referred to as individual-based or agent-based models. The individual's behavior, its movements for example, is specified by an algorithm, that describes how an individual responds to its neighbors, and possibly to its environment and its internal state. These behavioral rules are applied in turn to all individuals and integrated over time, usually by running a computer simulation. Thus, individual-based



Figure 1.4 – A shoal of maldives surgeon fish (*Acanthurus leucosternon*). Photo by: Uxbona (Wikipedia)

models use a bottom-up approach (c.f. synthetic method, Pfeifer and Scheier 1999), that starts with the individuals and aims to explain the patterns at the group-level as emergent properties (Grimm 1999), which makes them perfect tools to investigate aggregation behavior of animals.

For more theoretical background on Eulerian or Lagrangian models, see e.g. Grünbaum and Okubo (1994).

1.3 Evolutionary algorithms

Evolutionary algorithms were developed as biologically inspired tools for optimization of engineering systems (see e.g. Bäck, Fogel, and Michalewicz 1997). Several techniques have been developed over time (evolutionary programming, Fogel et al. 1966; genetic algorithms Holland 1975; and evolution strategies, Rechenberg 1973) which share the common basic algorithm: Starting from a population of random solutions for a given problem, their performance (*fitness*) is evaluated. During (roulette wheel) *selection*, a set of solutions is picked randomly but based on their fitness values, such that good solutions have a higher probability to “survive”. In the following *recombination* the selected solutions are combined and occasionally altered randomly (*mutation*) to obtain a new population of solutions. By repeating fitness evaluation, selection and recombination, the average fitness in each generation of solutions increases. The process



Figure 1.5 – A school of *Selar crumenophthalmus* forming a tight “ball”. Photo by: Bo Pardeau (uwphotographyguide.com).

stops, when there is no improvement or the desired level of fitness has been achieved.

In this thesis, we will be using genetic algorithms to evolve schooling behavior. As our goal is to find the conditions under which schooling is beneficial, we vary the abilities and behaviors of a predator, and use the genetic algorithm to test if schooling is beneficial under the given conditions or not.

1.4 Embodiment and situatedness

The concepts of embodiment and situatedness (among others) have been proven very fruitful in guiding the development of models and robots in the field of embodied artificial intelligence (Pfeifer and Bongard 2007; Pfeifer and Scheier 1999).

Embodiment and situatedness couple an agent to the real world or, more generally, to its environment: An embodied agent possesses a physical body to act in the real world and a situated agent reacts to its environment according to the information it extracts through its own sensors. Biological agents, e.g. animals, are always embodied and situated. Therefore, in our biological models, the embodiment and the situatedness of the agents or individuals, are important aspects.

Historically, those concepts were developed when it became clear, that the purely computational approach of classical artificial intelligence was fundamentally flawed.

Classical artificial intelligence was successful in tasks such as playing chess or proving

mathematical theorems, i.e. tasks that could be described as formal systems because they reside in well defined (symbolic) domains. On the other hand, everyday tasks such as locomotion or object manipulation, that are typically performed in the real world, proved to be notoriously hard for classical artificial intelligence. Partly, because the brain is not a computer that does symbol manipulation. Instead, body and nervous system are inseparable, and behavior is not understandable looking only at either one of them. Instead, behavior is generated by the interaction of body and mind with the environment, i.e the real world.

Embodied artificial intelligence adopts the synthetic methodology of “understanding by building”, by creating artificial systems, usually robots, to reproduce certain aspects of natural systems. In this thesis, however, we are not concerned with robots, but with individual-based simulations. However, investigation of group behavior by means of individual-based models also employs the synthetic approach.

Here, in this thesis, we will do a first step in transferring the concepts of embodiment and situatedness from field of embodied artificial intelligence to the individual-based modeling approach and apply it to fish schools.

1.5 Biological aspects of fish schools

Fish schools express a great variety of patterns (see Figs. 1.3-1.5 for a few examples) and it is estimated that around 25% of the species, e.g. herring and anchovy, aggregate throughout their life (obligate schooling, Shaw 1978), and even more, e.g. cod and saithe, form schools some of the time (facultative schooling). Often, it is distinguished between shoaling, which refers to any kind of social aggregation of fish (Fig. 1.4), and schooling, which more specifically denotes synchronized, i.e. polarized, groups of fish that move (Fig. 1.3, Pitcher 1983).

In the remainder of this section we review briefly the biological literature on why and how fish school. For more thorough background information we suggest Pitcher and Parrish (1993) and Parrish and Hamner (1997).

1.5.1 Benefits - Why do fish school?

The fact that many species of fish live in schools at least for some time suggest that schooling is beneficial to the individuals that constitute the group (Pitcher and Parrish 1993). The following paragraphs provide an overview on the most important benefits but also disadvantages.

Predator avoidance and dilution of attack. Because of the optical properties of water (absorption and scattering) groups cannot be detected from much larger distances than single individuals (Murphy 1980). Therefore, it takes a predator longer to find prey, if it is grouped rather than randomly dispersed (predator avoidance, Partridge 1982). If the predator, once it detected a school, can only eat one individual or small proportion of the group, while the others can flee, schooling is a good strategy (Treisman 1975). Furthermore, the larger the school, the lower the probability for an individual fish to be the one that is attacked (dilution of attack, Turner and Pitcher 1986).

Predator evasion. Fish have evolved a number of strategies, to evade a predator, among them forming very dense balls (Fig. 1.5), mills and vacuoles around the predator. The most impressive

behavior is probably the flash expansion, where the individuals rapidly swim in all directions, that looks like an explosion (see e.g. Pitcher and Wyche 1983 or Pitcher and Parrish 1993 for an overview).

Predator confusion. Connected to the evasion strategies is the confusion effect (Milinski and Heller 1978), which denotes the inability of the predator to visually lock onto one target (Landeau and Terborgh 1986) because of the sensory overload generated in the predators visual system (Broadbent 1965).

Predator detection. Fish in schools are able to detect predators earlier because the task of watching for predators is shared among many individuals ('many eyes' hypothesis, Bertram 1978) and thus evade it earlier than single individuals. This is, because fish observe each others behavior closely. If a fish detects a predator (or food, see next paragraph), it adapts its behavior, which is detected by its neighbors, thus effectively "sharing" the information.

Foraging advantages. Schooling also provides two mechanisms that improve the foraging success of group members. Individuals find food faster because of the 'many eyes' effect (Pitcher and Magurran 1982) and, because they are better protected against predators than solitary individuals, they can also allocate more time to feeding (Magurran and Pitcher 1983).

Hydrodynamic benefits. Whether there are hydrodynamic benefits is still debated (see e.g. Weihs 1973 or Partridge and Pitcher 1979), but it seems unlikely that they were a primary reason for the evolution of schooling behavior (Pitcher and Parrish 1993).

Disadvantages. Large predators, such as sea mammals, exploit the tendency of prey to form dense balls (Norris and Dohl 1980). Furthermore, individuals within a school, are also competitors, e.g. for food (Bertram 1978).

Group size. The benefits and costs of schooling behavior depend on the group size, i.e the number of individuals in the school. The effectiveness of predator confusion, for example, is higher for larger groups (Landeau and Terborgh 1986), but in larger groups competition for food is also higher (Bertram 1978).

Position within the school. But also the position of the individual within the group is important when balancing costs and benefits. For example, positions in the interior are considered the safest location (e.g. Bumann 1993), but for hungry animals the most preferable positions are those at the front, because here they will encounter food first (e.g. Krause 1993a).

Size sorting. In schools, even if they consist only of one species, individuals vary in body size. Body size affects both the foraging abilities and the predation risk. Small fish, for example, have higher energetic requirements (Wootton 1994) and are at the same time at a disadvantage when competing for food with larger companions (Krause 1994b). On the other hand, large individuals, if among small ones, are more conspicuous and therefore less protected by the confusion effect (Peuhkuri, Ranta, and Seppä 1997). Therefore, individuals seem to prefer to

school with others of similar size, which leads to size-assorted schools (Peuhkuri 1999) and to size-segregation within schools (Pitcher, Magurran, and Edwards 1985).

1.5.2 Mechanisms - How do fish school?

Here we will review very briefly properties of fish schools and sensory systems in fish, in order to utilize them for the development of schooling models.

Properties of fish schools

Fish schools are cohesive aggregations of tens up to millions of fish with clearly defined borders. Although the inter-individual spacing is very variable, it is usually around one body-length. Visually, the most striking property of fish schools is their polarization and synchronization, the parallel orientation of the individuals and their seemingly choreographed movement. Despite this order, individuals change positions frequently and they are not arranged regularly (like the atoms in a crystal, Partridge 1982). Indeed, the movements of any two individuals in a school are only weakly correlated (Aoki 1980; Partridge 1980). These results suggest, that schools have no leader. Instead, the individuals match their speed and orientation to the average of their neighbors. In other words, the entire school is the leader and the individuals are the followers (Niwa 1996).

Visual (e.g. Osborn 1997) and acoustic methods (e.g. Greene and Wiebe 1997) have been used to capture the distribution of individuals and other statistics of schools of many thousands of individuals (e.g. Misund 1993), to determine the detailed positioning of neighbors (e.g. Partridge et al. 1980) and also to track the trajectories of individuals (e.g. Hemelrijk et al. 2010). These studies show that, first, there is great variation both within and between schools and between species. But, second, that qualitatively characteristics are very similar across taxa, thus suggesting common underlying mechanisms (Parrish and Viscido 2005).

Conclusions for modeling schooling interactions. It has long been hypothesized that fish engage in social interactions, i.e. react by few simple behavioral rules to movements of their neighbors (Breder Jr. 1954; Partridge 1982) to achieve the schooling behavior we observe.

Clearly, an *attractive* force must exist in order for a school to be formed in the first place, and for the individuals to stay close to each other (Morrow Jr. 1948).

Individuals maintain an empty space around themselves, thus there must also be a *repulsive* force. The size of this area is different between species and it is bigger for larger individuals. The distance to the nearest neighbor is, on average, around one body length (Partridge 1982) but this varies a lot within and between schools and depends on circumstances, i.e. whether schools are under predatory attack or not. The avoidance of very close neighbors must be strong, because even during sudden and fast maneuvers individuals rarely collide.

Attraction and repulsion are contrary to each other. While repulsion is evidently stronger at shorter distances or for the closest neighbors, respectively, attraction must be stronger than repulsion between individuals that are further apart (Breder Jr. 1954).

The fact that in a fish school all members face in the same direction has been explained differently. For example Morrow Jr. (1948) reasoned that fish use vision to orient themselves parallel to their neighbors. On the other hand, the parallel orientation could be a by-product of

the forward movement or it could be induced externally, e.g. if the fish have a common goal or if there is a water current (as fish tend to head upstream).

Sensory systems in fish

In order to school (but also for other activities), fish require sensory systems that allow them to assess quickly and accurately the small changes in their neighbors positions and headings relative to their own.

It has been speculated already very early, that vision is probably the most important sensory modality for schooling (Morrow Jr. 1948). But also the lateral line was suspected to be important, at least for avoiding collisions (Breder Jr. 1954). Later, Partridge and Pitcher (1980) have shown, that fish are able to school even without vision or without the lateral line, but not without both of them. Although there is indication that also other senses are also involved in schooling (e.g. olfaction, Pitcher and Parrish 1993) vision and the lateral line are generally considered to be the most important ones.

Because the lateral line only works over relatively short distances of 1-2 body lengths (Larson 2009) its main functions is probably to avoid collisions and, because it senses pressure waves and water flow, to determine the speed and orientation of nearby neighbors (Partridge and Pitcher 1980). Vision is considered more important for longer range interactions, for example to keep the school from splitting, and to maintain position and angle between fish (Partridge and Pitcher 1980). Because of scattering and absorption, the usefulness of vision also degrades quickly with distance (Pitcher and Parrish 1993), such that it is only effective for a few meters (depending on water conditions).

Conclusions for modeling individual perception. To guide the modeling process, it is important to know which information about the environment is available to fish, otherwise our models might include unrealistic assumptions. First, because of the limited range of their senses in water, fish can only perceive their local environment. They are clearly able to recognize their conspecifics and it is reasonable to assume, that using vision and the lateral line fish can assess direction and distance to neighbors (i.e. their position), as well as their orientation and speed.

1.6 Modeling fish schools as self-organized systems

Computer-based models have been used to investigate aggregation behavior of animals in general and schooling in particular for two reasons.

First, the biological mechanisms underlying schooling behavior are still not well understood. Partly, because it is difficult to record the behavior of the individuals, especially for large groups. But mainly, even if detailed data were available, because the individual behaviors cannot be determined from the behavior observed at the group-level. Group behavior, by its nature, is a result of the interactions between its members and consequently cannot be analyzed by examining a single individual. Therefore, it is necessary to create a behavioral model of the individual that includes our hypotheses about the animal's responses to its neighbors.

Second, because of the complex interaction among the individuals in a group, we cannot determine the outcomes of such a model directly, i.e. by merely looking at the rules of interaction. Instead, we have to determine the behavior by means of computer simulations. The emerging

patterns can then be compared to the properties of real schools to validate our assumptions, and to get a deeper understanding of “how” the animals form the groups we observe in nature.

Since the first attempts on describing how fish school (Breder Jr. 1951; Parr 1927; Shaw 1978) and the first simulation models thereof (Inagaki, Sakamoto, and Kuroki 1976) the focus was on the question, which individual behaviors lead to schooling. Consequently, the models are kept as simple as possible in order to determine which behaviors are necessary: individuals are identical and they react to their neighbors by adjusting speed and orientation only.

All those models share a common structure that consists of three components: First, a *selection* criterion describes by which neighbors an individual is influenced. Second, a set of rules specifies the behavioral *response* of an individual to an influential neighbor. And third, an algorithm that determines how the (possibly conflicting) behavioral responses of an individual to all its influential neighbors are *mixed*.

Selection of interaction partners. Concerning selection almost all models employ either a criterion based on a maximal interaction range (often with a blind field at the individual’s back, see Fig. 2.1 and e.g. Couzin et al. 2002; Niwa 1994; Reuter and Breckling 1994) or one that restricts the interaction to the n nearest neighbors, sometimes referred to as numerical preference (e.g. Aoki 1982; Huth and Wissel 1992; Viscido, Parrish, and Grünbaum 2005).

The intuition behind both approaches is that individuals are not omniscient. Their perception of others is limited by distance and by the number of neighbors their sensory systems can handle.

In what follows we will refer to models using a maximal interaction range as *metric models* (because they use a criterion based on metric distance) and to those restricting the interaction to the n nearest neighbors as *topological models* (because they use a criterion based on topological distance). For more information on the differences between metric and topological approaches see Giardina (2008).

Mixing if the influences of the interaction partners. Concerning the mixing element, most models use a sum-of-forces approach, which essentially averages the behavioral responses to the influential neighbors (e.g. Aoki 1982; Reuter and Breckling 1994; Viscido, Parrish, and Grünbaum 2005). Sometimes, the individuals are weighted differently, e.g. according to their position (Huth and Wissel 1994b), to represent a priority in the selection of the influential neighbors.

Behavioral response. All models implement attraction and repulsion, in order for groups to form and to avoid collisions within the group. To achieve a stable individual spacing, some form of balance of force must exist, which can be achieved by using short-range repulsion and long-range attraction (e.g. Warburton and Lazarus 1991). Most models found that a weak alignment force is needed in addition (e.g. Aoki 1982) in order to get polarized schools. Thus the “rules” that describe the behavioral response to the neighbors are:

Repulsion: Move away from neighbors that are too close.

Alignment/Velocity Matching: Adjust the heading and the speed to match that of nearby neighbors.

Attraction: Move towards neighbors that are further away.

The distance dependency of these responses has been implemented in two ways. First, by using so called behavioral zones within which neighbors are treated equally (e.g. Huth and Wissel 1992). The response is either repulsion, alignment or attraction, depending on the distance to the influential neighbor.

Second, by using continuous weight functions (e.g Reuter and Breckling 1994; Warburton and Lazarus 1991) the response to an influential neighbor changes gradually with distance and is usually a combination of repulsion and alignment or attraction and alignment.

Individual-based models of schooling contain a number of assumptions about poorly-understood aspects of grouping behavior, for example the details of social interactions, i.e. the behavioral responses, but also the selection of influential neighbors. Therefore, there is great variability across models in the details how those are implemented.

1.6.1 General properties of schooling models

Despite the differences among the schooling models, there are several general properties that hold for all of them.

For example group density is affected by relative strength of repulsion and attraction, but also depends on the number of interacting individuals:

- Increasing attraction or weakening repulsion leads to denser groups (e.g. Mogilner et al. 2003; Warburton and Lazarus 1991).
- Large groups (that consist of a larger number of individuals) are also denser. This is because more individuals are attracted to each other, i.e. a larger number of individuals that push from periphery towards the center of the school. This is found in metric models (e.g. Warburton and Lazarus 1991) but also to some extent in topological models (e.g. Viscido, Parrish, and Grünbaum 2005). This is also discussed in chapter 2.
- Likewise, increasing the number of influential neighbors in topological models leads to denser schools (e.g. Viscido, Parrish, and Grünbaum 2005). Similar results are described in chapter 4.

The relative strength of alignment, on the other hand, affects polarization of the individuals and the speed of the school:

- If the alignment tendency is weak, the school loses its coherence and the polarization of the individuals is low, which results in a slow group speed, because individuals head into different directions and are continually turning to avoid neighbors. Increasing the strength of alignment leads to polarized groups whose speed is increased, because here individuals agree on a common swimming direction (e.g. Viscido, Parrish, and Grünbaum 2004). The connection between polarization and group speed is also discussed in chapter 2.
- If the range of distances over which individuals align with neighbors is small (compared to the range of attraction), schools start to form a ring or a torus (“milling”) because they align only with their immediate neighbors but are still attracted to others further away, which causes the group to form a loop (Couzin et al. 2002; Gautrais, Jost, and Theraulaz 2008). If alignment is effective over larger distances, on the other hand, parallel orientation becomes more important and the formation of a loop becomes improbable.

A few studies explored the impact of individual differences on the group-level behavior and on the positioning of the individuals:

- Individuals with stronger attraction or weaker repulsion responses, i.e. those that have a shorter preferred nearest neighbor distance, end up in the center of the group, others are pushed to the periphery (Couzin et al. 2002; Romey 1996). Essentially the same results, but connected to the body size of the individuals, are demonstrated in chapter 3.
- Individuals with a higher preferred speed move to the front of the group, whereas those with a higher turning rate slow down and end up at the rear (Couzin et al. 2002).

This is only a small part of the findings, but they are those we think are important to get a basic understanding how the selection of influential neighbors, the behavioral responses and their mixing influences the behavior at the group-level.

1.7 Artificial evolution of schooling behavior

The models reviewed so far focused on the mechanisms that generate schooling behavior, i.e. they focused on the question *how* schooling behavior emerges. However, individual-based models can also be used to investigate the circumstances under which schooling behavior is beneficial, i.e. to help elucidate the question *why* schooling behavior evolved.

This can be done at least in two ways. First, by introducing a predator into an individual-based schooling model. Here, the effectiveness of strategies both for the prey as well as for the predator can be tested directly (Nishimura 2002; Zheng et al. 2005).

A second approach uses artificial evolution (e.g. genetic algorithms) to generate or adjust the behavioral responses of the individuals. Artificial evolution is used generally to optimize a system according to a fitness function. In the context of schooling, there has been one failed attempt to evolve schooling directly (Zaera, Cliff, and Bruten 1996), using an engineered fitness function that should have rewarded schooling behavior. The goal of the evolutionary process was to optimize the parameters of a neuronal controller that steered the individuals. However, while the method was successful to generate simple shoals (without the parallel alignment of the individuals), it was impossible to evolve schooling behavior. The conclusion was surprising: Apparently, we do not know how to come up with a fitness function that induces schooling, but not other types of aggregation behavior, i.e. although visually we can recognize schooling instantly, we cannot put that knowledge into an objective function.

An alternative approach is to use an “implicit fitness function”, i.e. a predator. This has been done by Oboshi et al. (2002) but only to evolve evasion strategies and not schooling behavior in itself, as basic schooling behavior was prespecified. Such an experiment gives insight as to which evasion strategies are beneficial, but it cannot explain why the fish school in the first place.

1.8 Outline and contributions of this thesis

This thesis is organized around 4 papers, 3 of which have been published in international scientific journals and proceedings of conferences. The first two introduce embodiment into individual-based simulations, the second two focus more on situatedness, i.e. how individuals or a predator perceive their environment.

1.8.1 Embodiment

So far, in almost all simulations of schooling individuals are modeled as mass-points, because agent movement was considered more important than their substance (Parrish and Viscido 2005).

Here we will develop a new model, where individuals are represented as lines (reflecting both body length and its elongated form). Furthermore, size and form of the individual is taken into account in the behavioral response, e.g. larger individuals have a larger personal space and thus avoid neighbors a larger distances.

In chapter 2 we study how body size and form of artificial fish affect social organization of schools, i.e. group form, density, polarization, turning rate and speed, in schools consisting either of large or small individuals.

In chapter 3 we investigate how differences in body size lead to size segregation in heterogeneous schools of different ratios of large and small individuals. We compare the patterns to when individuals choose neighbors according to their familiarity (kinship) or by similar body size (active assortment) and in combination with risk avoidance (where small individuals avoid larger neighbors more strongly).

1.8.2 Situatedness

Fish usually perceive only a small part of the school. This has been modeled using either a maximal interaction range (metric models) where individuals interact with all those located within this range, or by restricting the interaction to the n nearest neighbors (topological models).

Surprisingly often, in order to enhance stability and to avoid fragmentation of schools, model parameters (such as interaction range) were chosen such, that an individual interacted with a large fraction of the group (e.g. Huth and Wissel 1992; Reuter and Breckling 1994; Romey 1996; Warburton and Lazarus 1991).

However, in reality, even for a smaller interaction range or a lower number of nearest neighbors, many individuals might not be perceivable, although they are within sensory range, because of masking by closer neighbors. Interestingly, this was already recognized very early (Breder Jr. 1954; Huth and Wissel 1994a), but has never been incorporated into schooling models so far.

As an extension to our model, we implemented such masking of neighbors. Here, individuals can only perceive (and interact with) those that are not hidden behind closer neighbors, thereby making the model better situated.

In chapter 4 we study, how such “obstructed perception”, which restricts the interaction to the local environment of the individual, influences the social organization of schools.

By introducing a predator in our model (chapter 5) we study the conditions under which schooling protects the individuals from predation. In contrast to other studies, that were concerned with the evolution of predator evasion strategies, in our model the individuals are not aware of the predator, because the purpose of our model is to determine the conditions necessary for schooling to be of “passive” advantage. Specifically, in chapter 5 we describe whether predator avoidance and predator confusion were present in our model, depending on the perceptual abilities of the predator, its speed and the handling time required to consume a prey.

1.8.3 Implications

Chapter 6 summarizes our findings and the conclusions that can be drawn from them, finalizing the implications of embodiment and situatedness on the social organization of fish schools.

Chapter 2

Collective Effects of School Size, Body Size and Form¹

Abstract

Individual-based models of schooling in fish have demonstrated that, via processes of self-organization, artificial fish may school in the absence of a leader or external stimuli, using local information only. We study for the first time how body size and body form of artificial fish affect school formation in such a model. For a variety of group sizes we describe how school characteristics, i.e. group form, spread, density, polarization, turning rate and speed, depend on body characteristics. Furthermore, we demonstrate that nearest neighbor distance and turning rate of individuals is different for different regions in the group, although the agents are completely identical.

Our approach shows the significance of both self-organization and embodiment in modeling of schools of artificial fish and, probably, in structuring schools of real fish.

2.1 Introduction

In studies of artificial life and artificial intelligence the effects of self-organization and embodiment are important topics. In the present paper we investigate both aspects in the context of simulated artificial fish schools. We analyze how self-organization may lead to emergent behavioral phenomena at different group sizes (Camazine et al. 2001) and how this process may be affected by characteristics of the body and may influence collective behavior (Pfeifer 2000; Pfeifer and Scheier 1999). Several individual-based models of schooling in fish (Aoki 1982; Couzin et al. 2002; Huth and Wissel 1992, 1994b; Niwa 1994; Reuter and Breckling 1994; Romey 1996; Vabø and Nøttestad 1997) have revealed that artificial fish, which use local information only (like flocking birds, Reynolds 1987) may school in the absence of a leader and external stimuli. Further, some of them have shown certain collective effects of school size, but the origination of these effects have not been explained. By studying both group size and body characteristics (forms and sizes), we hope to obtain insight in the processes that lead to these collective effects.

¹appeared as H. Kunz and C. K. Hemelrijk (2003). „Artificial fish schools: collective effects of school size, body size, and body form.“ In: *Artif. Life*. 9.3, pp. 237–253

Our model is inspired by those from Huth and Wissel (1992, 1994b), Reuter and Breckling (1994) and Niwa (1994). In these models schooling is a consequence of the tendency of fish to avoid others that are close, to align their body to those at intermediate distances and to move towards others that are far away. Shaw (1970) already suggested such distance dependent mechanisms and distinguished between polarized, coordinated 'schools' and non-polarized, non-coordinated 'shoals'. Here, we investigate the former only.

In earlier models of fish schools, fish are represented as points and their regions of repulsion, aligning and attraction are concentric and circular. This does not reflect the form and size of the agent's body nor its sensory capabilities. Modeling the agent's body with its sensory characteristics may alter the way the agent is perceived by others as well as the way in which it perceives its neighbors itself. Therefore, we compare schooling behavior of artificial fish represented as lines to those represented as points. Furthermore, not only vision, but also the lateral line is used in schooling (Bleckman 1993; Partridge and Pitcher 1980). The lateral lines consist of a series of hydrodynamic sensors along both sides of the body (Bleckman 1993). They detect stimuli (i.e. changes in water flow) close to the body only. We reflect this in the model by making the shape of the repulsion and aligning areas elliptic in form. Therefore, we compare the collective behavior between artificial fish with circular areas of aligning and repulsion versus those with oval-shaped ones. Further, we investigate artificial fish of two different body sizes. Here, we follow the findings by Olst and Hunter (1970), that larger fish have larger repulsion areas, but the increase with body size is less than proportional.

In sum, we compare the collective behavior of artificial fish of different body size and form in increasing detail for various group sizes. Apart from traditional statistical measures we use also measures developed by ourselves (i.e. a measure of spatial homogeneity, of the relative location of the center of gravity within the school, and of group form). We will explain how self-organization and embodiment influences collective patterns of artificial schools of different sizes. Subsequently, we will indicate how these results may guide studies of real fish.

2.2 Methods

Our model contains aspects of several models by others. Like in the model by Huth and Wissel (1992), fish react to others by repulsion, by aligning and by attraction. In correspondence to Reuter and Breckling (1994) and Niwa (1994) these behavioral tendencies are weighted according to distance, and thus result in graded transitions between the different motivations.

Fish schools have been modeled in 2-D as well as in 3-D. Comparing a particular 2-D model (Huth and Wissel 1992) to a 3-D one (Huth and Wissel 1994b), no additional phenomena were obtained in the 3D-model. Therefore we decided to implement our model, SchoolingWorld, in 2-D.

2.2.1 The Model

The model consists of a world that is continuous (not a grid) in which artificial fish can move. The environment is homogeneous without structure. Time proceeds in discrete steps Δt . Each time step all artificial fish are activated sequentially in random order. Note that for parallel activation (where all agents are activated simultaneously) the same results are obtained. The model was implemented in C. Octave and Gnuplot were used for data-analysis.

Position, Speed, and Heading

At the beginning of the simulation, a certain number of artificial fish are put randomly in a starting area of $2.5 \times 2.5\text{m}$ and are given a random orientation, which was chosen between 0 and 90° in order to result in a single school. The initial speed of the agents was set to v_{avg} (see Tab. 2.1).

At time t agent i is located at position \mathbf{x}_i^t and moves with a velocity \mathbf{v}_i^t during one simulation step Δt .

$$\mathbf{x}_i^t = \mathbf{x}_i^{t-\Delta t} + \mathbf{v}_i^t \Delta t \quad (2.1)$$

The velocity \mathbf{v}_i^t is determined by the agent heading α_i^t (orientation of the vector \mathbf{x}_i^t) and by the speed v_i^t (length of the vector \mathbf{v}_i^t) as follows

$$\mathbf{v}_i^t = \begin{pmatrix} v_i^t \cos \alpha_i^t \\ v_i^t \sin \alpha_i^t \end{pmatrix} \quad (2.2)$$

Similar to certain models of fish schools (Aoki 1982; Couzin et al. 2002; Huth and Wissel 1992, 1994b), the speed v_i^t of agents does not depend on that of other agents, but is an independent stochastic variable. It is drawn from a Gaussian probability distribution $P(v_{\text{avg}}, v_{\text{sd}})$ each time step. The stochasticity is chosen to reflect unspecified variation in speed.

The heading α_i^t of agent i is determined by

$$\alpha_i^t = P(\underbrace{\alpha_i^{t-\Delta t} + \omega_i^t \Delta t}_{\alpha_{i,\text{avg}}^t}, \alpha_{\text{sd}}) \quad (2.3)$$

where $\alpha_i^{t-\Delta t}$ is the agent's heading in the previous simulation step and ω_i^t is its rate of rotation, which depends on the interaction with the other agents (see following section). α_i^t is again drawn from a Gaussian distribution $P(\alpha_{i,\text{avg}}^t, \alpha_{\text{sd}})$.

Repulsion, attraction, and aligning

The artificial fish have three types of behavioral responses, namely repulsion (short distances), attraction (intermediate distance), and aligning (greater distances) (e.g. Breder Jr. 1954; Warburton and Lazarus 1991). This has often been modeled by splitting the region surrounding the agent into behavioral zones with discrete boundaries (e.g. Huth and Wissel 1992), therefore an agent triggers exactly one type of behavioral response in a neighbor. An alternative approach, which is adopted here, is the use of continuously varying distance dependent weight factors to determine the effectiveness of repulsion, aligning and attraction behaviors (e.g. Niwa 1994; Reuter and Breckling 1994). Thus, an agent triggers all three types of behavioral responses in a neighbor, although with different effectiveness.

In their experimental studies of real fish, Partridge and Pitcher (1980) have shown that the three behavioral responses are mediated by different sensory systems (lateral lines and visual system) to a different extend. Cutting the lateral lines makes it difficult for fish to align their swimming direction to others and to keep others at a minimal distance, whereas blindfolding fish impairs social attraction.

We assume that attraction, mediated by vision mainly, operates in the complete visual range around the agent apart from a “blind area” in the back with an angle of $\gamma = 60^\circ$ (Fig. 2.1A). For aligning, for which the lateral line is considered to be the most important sensory system,

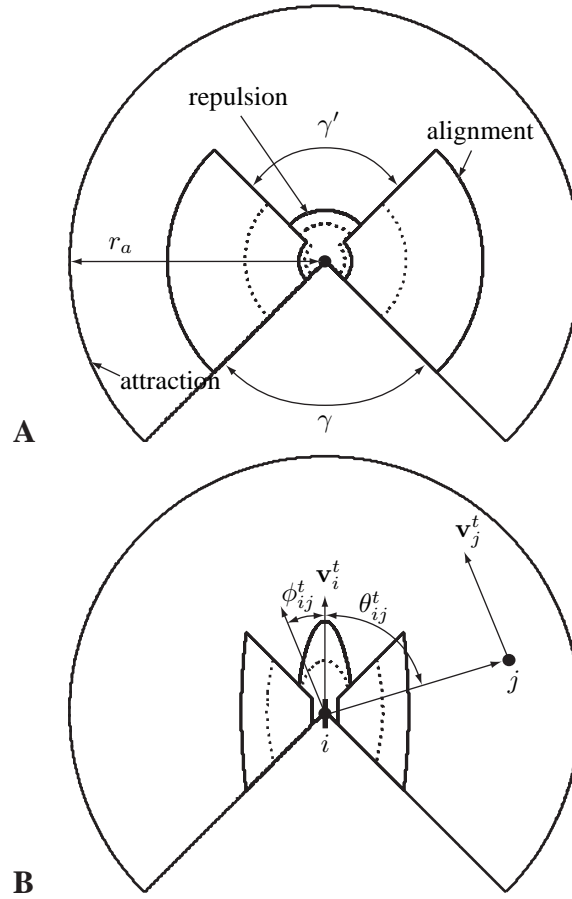


Figure 2.1 – Schematic representation of the different behavioral regions of an agent. The agent is located at the center. The outermost circle shows its visual range r_a , which can be divided into three functional areas, namely attraction, aligning, and repulsion. **A:** point-agents (gray indicates the attraction and repulsion regions of small agents, black of large ones). Note that line-agents are the same, but for a line representing their body instead of point. **B:** elliptic-agents; body size is indicated by the small line in the center. See text for further information.

Parameter	Symbol and value
Simulation time step	$\Delta t = 0.2\text{s}$
Average agent speed	$v_{\text{avg}} = 0.3\text{m/s}$
Standard deviation of agent speed	$v_{\text{sd}} = 0.03\text{m/s}$
Standard deviation of agent heading	$\alpha_{\text{sd}} = \frac{\pi}{72}\text{rad} \approx 2.5^\circ$
Default rate of rotation of the agents	$\omega^{\text{def}} = \pi\text{rad/s}$
Body length	Point agents: $b = 0.0\text{m}$ Large agents (line, elliptic): $b = 0.2\text{m}$ Small agents (line, elliptic): $b = 0.1\text{m}$
Scaling factor for repulsion	Large agents: $a_r = 2.0$ Small agents: $a_r = 1.0$
Scaling factor for alignment	$a_p = 1.0$
Scaling factor for attraction	$a_a = 1.0$
Repulsion range	Large agents: $r_r = 0.6\text{m}$ Small agents: $r_r = 0.3\text{m}$
Alignment range	Large agents: $r_p = 2.0\text{m}$ Small agents: $r_p = 1.0\text{m}$
Attraction range (visual range)	$r_a = 5.0\text{m}$
Eccentricity of repulsion and alignment regions	Point and line agents: $e = 0.0$ Large elliptical agents: $e = 4.0$ Small elliptical agents: $e = 2.0$

Table 2.1 – Simulation parameters.

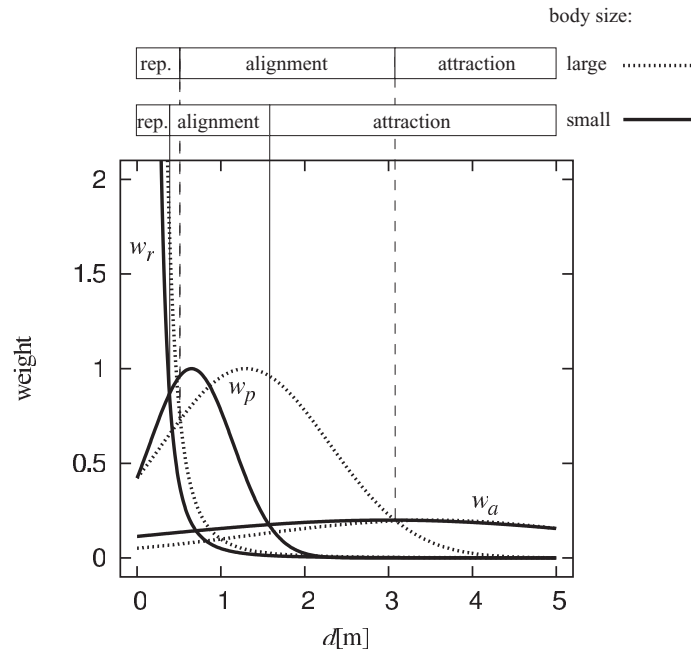


Figure 2.2 – Plot of the weight factors $w_r(d)$, $w_a(d)$, and $w_p(d)$ for small agents (solid lines) and large ones (dotted lines). d denotes the distance to the neighbor. Regions are classified into repulsion, aligning, and attraction by the largest of the three weight factors (top of figure).

there is an additional “blind area” at the agent’s front (Fig. 2.1A, $\gamma' = 60^\circ$). Thus the lateral line is most effective at the sides and it operates at intermediate distances. Repulsion, mediated by both lateral line and vision, operates in the complete visual range (Fig. 2.1A).

Repulsion implies that an agent i turns away from a close-by agent j with an rate of rotation (angular speed) of

$$\omega_r = \begin{cases} -\omega^{\text{def}} & \text{if } \theta_{ij}^t > 0 \text{ (avoid agent to the left)} \\ \omega^{\text{def}} & \text{otherwise (avoid agent to the right)} \end{cases} \quad (2.4)$$

where $\theta_{ij}^t = \angle(\mathbf{v}_i^t, \mathbf{x}_j^t - \mathbf{x}_i^t)$ (see Fig. 2.1B) and ω^{def} is the “default” rate of rotation of the agents (Tab. 2.1), reflecting their movement capabilities. Attraction implies that an agent i turns towards an agent j with a rate of rotation of

$$\omega_a = \omega^{\text{def}} \theta_{ij}^t \quad (2.5)$$

Note that, in contrast to repulsion, the rate of rotation ω_a caused by attraction is proportional to θ_{ij}^t . Aligning implies that agent i matches its orientation to that of agent j by turning with a rate of rotation

$$\omega_p = \omega^{\text{def}} \phi_{ij}^t \quad (2.6)$$

where $\phi_{ij}^t = \angle(\mathbf{v}_j^t, \mathbf{v}_i^t)$ is the angle between the orientations of the two agents (Fig. 2.1B). The actual behavioral reaction depends on the weights of repulsion w_r , attraction w_a and aligning w_p ,

$$w_r(d) = \min\left(\frac{0.05a_r}{d^3}, 10.0\right) \quad (2.7)$$

$$w_a(d) = 0.2a_a e^{-\left(\frac{d - \frac{r_a + r_p}{2}}{r_a - r_p}\right)^2} \quad (2.8)$$

$$w_p(d) = a_p e^{-\left(\frac{d - \frac{r_p + r_r}{2}}{r_p - r_r}\right)^2} \quad (2.9)$$

(see Fig. 2.2 and Tab. 2.1 for the parameters) due to the distance to the other agent

$$d_{ij} = \|\mathbf{x}_j^t - \mathbf{x}_i^t\| \quad (2.10)$$

The combined behavioral reaction, i.e. rate of rotation, of agent i due to the interaction with a single agent j is calculated as a weighted sum

$$\omega_{ij}^t = w_r(d_{ij}^t)\omega_r + w_a(d_{ij}^t)\omega_a + w_p(d_{ij}^t)\omega_p \quad (2.11)$$

The weight factors shape the behavioral reaction to depend continuously on the distance. Therefore, there is no discrete behavior switching. Nevertheless, for convenience, we label three behavioral regions after the largest of the three weighting factors (Fig. 2.2). When agent i perceives more than one other agent j (by either vision or the lateral line), its behavioral response (rate of rotation) is calculated as the average of the response it would display when considering each neighbor independently, i.e. the average of the rate of rotation caused by each of the agents j separately

$$\omega_i^t = \frac{1}{N_i} \sum_j \omega_{ij}^t \quad (2.12)$$

Here, N_i denotes the number of agents perceived by agent i . Note that ω_{ij}^t describes the behavioral reaction (rate of rotation) of agent i in response to the presence of agent j (not to be confused with the rate of rotation ω_j^t of agent j).

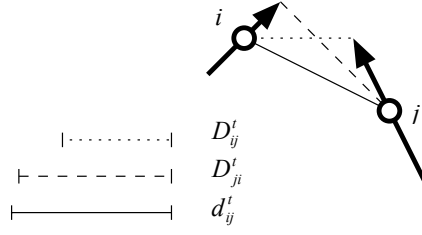


Figure 2.3 – Measures of distance between agents. d_{ij}^t denotes Euclidean distance between the centers of the two agents. D_{ij}^t and D_{ji}^t denote an alternative approach calculating agent distance, where both body size and form is reflected in agent distance (see text for details).

Body size and form

Three aspects of the agents were varied to reflect body characteristics. First, we represent the agent's body by a line of variable length b instead of a point (Tab 2.1). This does not change the agent's behavior directly, but it alters the way the agent is perceived by others as follows. Instead of using the distance between the agents' centers d_{ij}^t , to measure distance between two agents, the distance between agent i 's center and the nearest point of agent j , denoted as D_{ij}^t (Fig. 2.3) was used in (2.11). Note that D_{ij}^t and D_{ji}^t differ depending on the body size b (Fig. 2.3).

Second, as regards body size we follow the findings by Olst and Hunter (1970) that larger fish maintain larger inter-individual distances, but they are closer than would be expected if inter-individual distance would be proportional to the body size. This is modeled by increasing the sizes of the repulsion and aligning regions (by changing the values of a_r , r_r , and r_p , see Figs. 2.1 and 2.2, Tab. 2.1 and Eqs. 2.7 and 2.9). The range of attraction (mediated by vision) was kept identical.

Third, body form is modeled by including sensory characteristics of the lateral line, therefore changing the agent's perception of its neighbors. We assume that the perceptual field of the lateral line follows the body form; therefore the repulsion and aligning regions are elliptic rather than circular (Fig. 2.1B). This is achieved by redefining agent distance d_{ij}^t used in Eq. 2.11. Consider an agent j at position (u_j, z_j) relative to a coordinate system embedded in agent i , in such a way that the u -axis points in the heading direction α_i^t of agent i . For elliptic agents distance between agent i and j is defined as

$$e_{ij}^t = \sqrt{\frac{1}{e}u^2 + ez^2} \quad (2.13)$$

where e is the eccentricity (Tab. 2.1). Therefore, if agent j is located directly in front of agent i ($z = 0$), e_{ij}^t is smaller than d_{ij}^t and if agent j is at the side of agent i ($u = 0$), e_{ij}^t is larger than d_{ij}^t . Consequently, agents will avoid those neighbors that are ahead of them sooner (at a greater distance) than those that are at their side (conform the elliptic form of the repulsion region, see Fig. 2.1B). The same applies for the aligning region.

Thus, body size and form is modeled as follows in three levels of increasing detail (see Tab. 2.1):

Point-agents: Agents are modeled as points; body size is only reflected in the size of the regions of repulsion and aligning. Agents of larger size have larger regions of repulsion and aligning, but their range of attraction (their vision) is the same for all (see Fig. 2.1A, black: regions of large agents, gray: those of small agents).

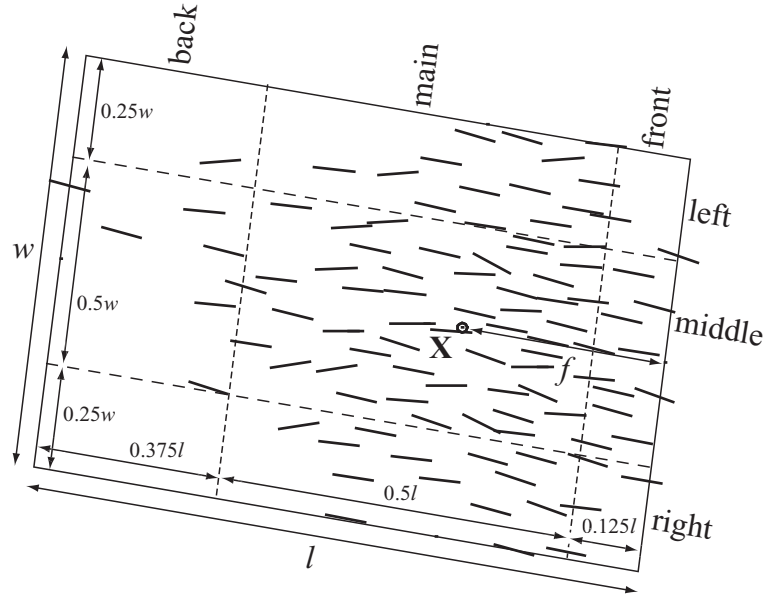


Figure 2.4 – The box method for obtaining measures of group width w , length l and front f . Dashed lines indicate the different regions of measurement.

Line-agents: Agents are represented as lines. Larger body size is reflected in longer lines and larger regions of repulsion and aligning (Fig. 2.1A).

Elliptic-agents: Agents are represented as lines. The regions of repulsion and of aligning are elliptic and are larger for large agents than for small ones. The region of attraction is circular and independent of body size (Fig. 2.1B)

Note that we included the line-agents as a kind of 'control', to study merely the effects of the representation of the agent's body as a line.

2.2.2 Experiments

For agents of a body length b of 0.2m (large) and 0.1m (small) and for all three types of body form we have studied eight population sizes of 3, 4, 6, 10, 25, 50, 75, 100 identical agents. Every simulation was repeated 25 times for random starting locations. For parameters see Tab. 2.1.

2.2.3 Measures

Each simulation step the following statistics have been calculated.

To measure group spread, we use the average distance of all agents to the center of the group, the so-called average center distance

$$c^t = \frac{1}{N} \sum_i \|\mathbf{X}^t - \mathbf{x}_i^t\| \quad (2.14)$$

where

$$\mathbf{X}^t = \frac{1}{N} \sum_i \mathbf{x}_i^t \quad (2.15)$$

denotes the center of gravity of the school. A similar measure, expanse, (i.e. average quadratic distance to the center of the group) was used by Huth and Wissel (1992).

To measure group density we use average nearest neighbor distance n_1^t (see for instance, Huth and Wissel 1992). We quantify the uniformity of the spatial distribution of agents, called 'homogeneity', by the average distance to the nearest neighbor divided by that to the second nearest neighbor

$$h^t = \frac{n_1^t}{n_2^t} \quad (2.16)$$

Greater homogeneity of spatial distances among agents is reflected by values close to one, whereas high irregularity (low homogeneity) of agent distribution results in lower values.

To quantify the coordination of the heading directions of the agents, we calculate the square root of the mean quadratic angle deviation of each fish to the average heading α_{avg}^t of the group

$$p^t = \sqrt{\frac{1}{N} \sum_i (\alpha_{\text{avg}}^t - \alpha_i^t)^2} \quad (2.17)$$

where α_{avg}^t is the average heading of the agents. p^t is usually referred to as 'polarization' (Huth and Wissel 1992), but we call it 'confusion', since higher values indicate greater disorder. Note that by 'homogeneity' we denote spatial uniformity of the locations of the agents, whereas confusion and polarization measure the coordination (unidirectionality) of the headings the agents.

Further, group speed v_g^t is defined as speed of the center of gravity \mathbf{X}^t of the group; the group turning rate T_g^t as the (absolute) rate of change of direction of the group.

To measure school form we enclose the complete school by the smallest rectangle oriented parallel to direction of movement of the group (Fig. 2.4) and characterize group form by the length l^t , the width w^t , and their quotient q^t (width divided by length). To indicate the relative place g^t of the center of gravity \mathbf{X}^t in the school, we use the distance of the center of gravity to the front (called front length f^t) divided by total length l^t .

In order to detect spatial variations, we partition the group in two ways: the left, middle, and the right part, and the front, middle, and the back section (Fig. 2.4). In each of these parts we calculate the average agent turning rate (i.e., the (absolute) rate of change of the agents heading direction) and average nearest neighbor distance separately. We denote average agent turning rate by T_f^t and average nearest neighbor distance by n_f^t . The lower indices denote the section (f : front, n : main, b : back, l : left, m : middle, and r : right).

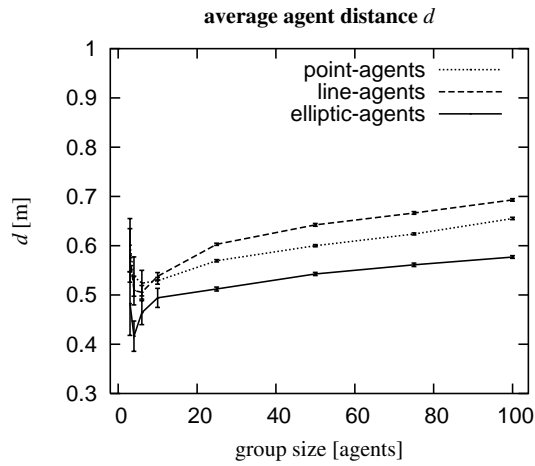
Per simulation the measures were averaged over the time-steps 2000-3000 (thus omitting the transitory period). Averages and their standard errors over 25 runs are plotted in the figures below. We discuss only the results that significantly different as can be derived from the small size of the standard errors. Further, we only evaluate runs where the agents aggregate in a single school. This was the case in 98.9% of the simulations.

2.3 Results

2.3.1 General effects of group size

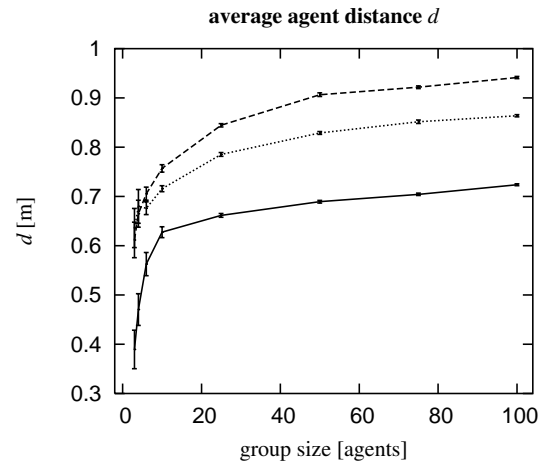
As a direct consequence of the larger number of individuals in larger schools, the average distance to the center increases with school size (Figs. 2.5AB), because a larger group covers

small agents ($b = 0.1\text{m}$)

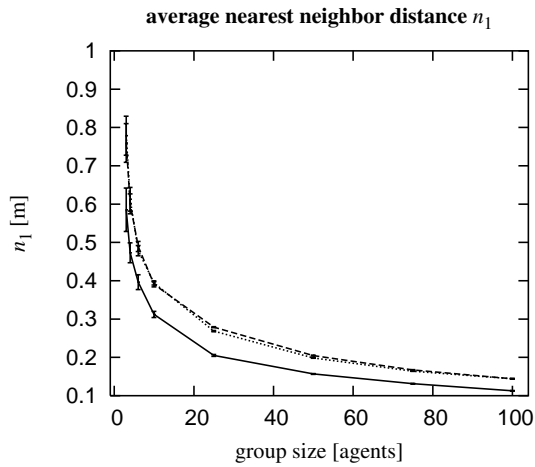


A

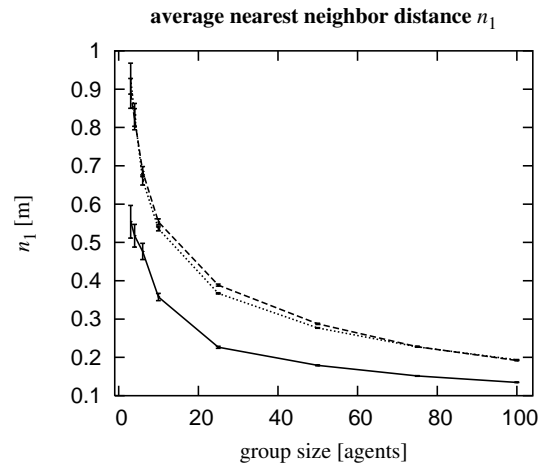
large agents ($b = 0.2\text{m}$)



B



C



D

Figure 2.5 – Distance measures and their standard errors for different sizes of groups of agents that are small (A, C) and those that are large (B, D).

a larger spatial area. Nevertheless the nearest neighbor distance decreases (Figs. 5CD) for increasing group size, due to the increased attraction among the larger number of group members, which leads to a denser packing of agents.

Because agents do not align directly with more remote group members in a larger group, confusion (mean angular deviation) increases (Figs. 2.6AB), and this leads to a lower speed of the group (Fig. 2.6CD). The turning rate of larger groups is lower (Fig. 2.6E, data for large agents are similar, but not shown). This is a consequence of the greater number of individuals that have to coordinate in order for the complete group to turn.

The center of gravity is significantly found in the front half of the school: The distance of the center of gravity to the front divided by the distance to the back was always smaller than 0.9 (for an example see Fig. 2.4). There are two causes for this. First, due to the constant speed, agents cannot catch up once they lag behind. Second, agents near the front have few individuals ahead of them. Therefore they have a lower tendency to move straightforward, but they may turn either left or right, wherever they perceive more neighbors. Consequently, their turning rate is higher compared to agents in the main and the back region, which are also attracted to others ahead (Figs. 2.7BD). Due to their increased turning rate, the front-agents slow down slightly which leads to crowding at the front. Also turning rate is lower at the sides than in the middle part of the school (Fig. 2.7F), especially for the elliptic agents.

The finding that the center of gravity is found in the front half of the school is also reflected in the relative nearest neighbor distances in different parts of the group (Fig. 2.7AC). Nearest neighbor distance is lowest in the central part and highest in the back, whereas it is intermediate at the front. It is also lower in the middle part, compared to the sides (Fig. 2.7E).

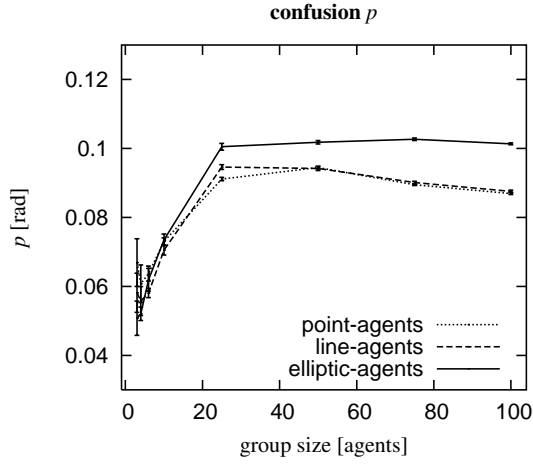
Increasing group size leads to an increase in both the width and length of the group (Figs. 2.8A-D). The width of the group increases slower at larger group sizes (Figs. 2.8AB), whereas the length of the group grows almost linearly with group size (Figs. 2.8CD). This may be due to the fact that in wide groups there is a strong attraction to the center among peripheral agents. This results in a strong inward movement of the agents located at the sides, whereas there is no similar mechanism for agents in the front or at the back of the school, because of their constant speed. Therefore, larger groups are longer than wide (Figs. 2.8ABCD).

2.3.2 Effects of body size and form

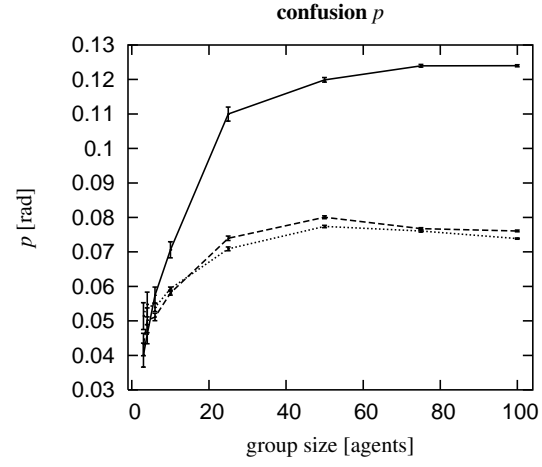
Larger agents are usually significantly further apart than smaller ones (as measured by average distance to the center and nearest neighbor distance, note the small values of the S.E. in Figs. 2.5A-D). This is due to their larger body size and repulsion area. For a similar reason, when comparing between different agent-types of the same body size, line-agents are significantly further apart than point-agents. For point- and line-agents, nearest neighbor distance is approximately the same, whereas average center distance is larger for line-agents. This arises because line-agents swim at larger distances behind each other, while swimming side by side they stay equally close as point-agents. Elliptic-agents swim significantly closest together (side by side) due to their narrow and lengthy (elliptic) repulsion region (Fig. 2.1B).

The uniformity of distances (i.e. homogeneity) among group members (measured in terms of the ratio of the distances to the first and second nearest neighbor) is weaker the more asymmetric the body form is. Thus, homogeneity decreases from point, via line- to elliptic-agents (Fig. 2.6F, similar for small agents, data not shown).

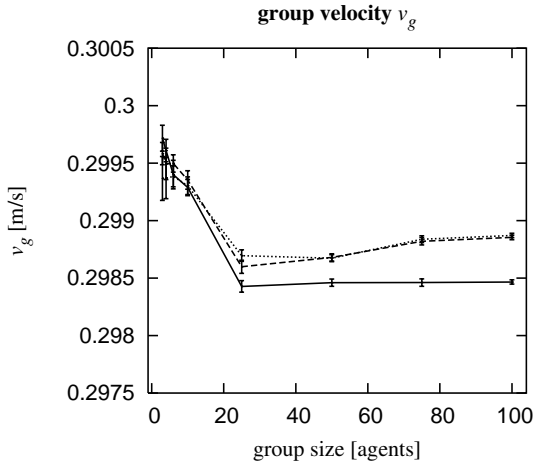
Comparing between groups of large and small agents group turning rate appears to be simi-

small agents ($b = 0.1\text{m}$)

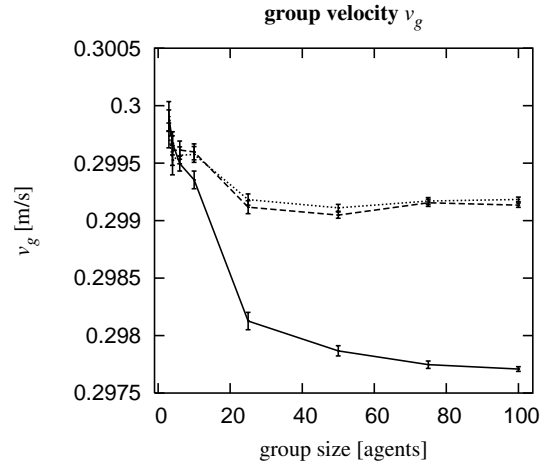
A

large agents ($b = 0.2\text{m}$)

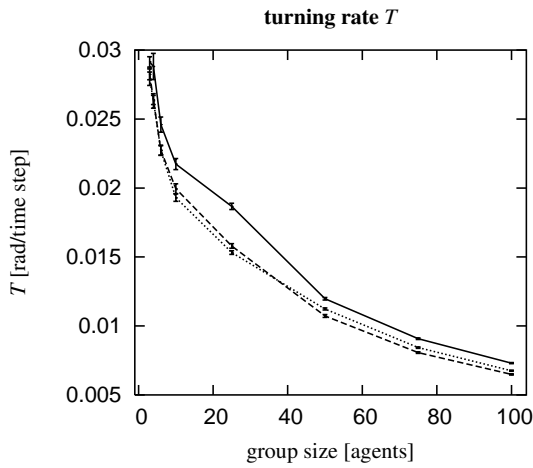
B



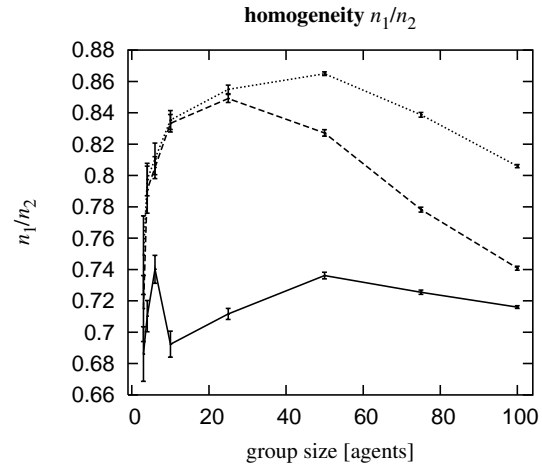
C



D



E



F

Figure 2.6 – Mean values and standard errors of confusion (A, B), group speed (C, D) group turning rate (E), and homogeneity of distances (F) of groups of large agents (right panels) and of small ones (left panels) for different group sizes.

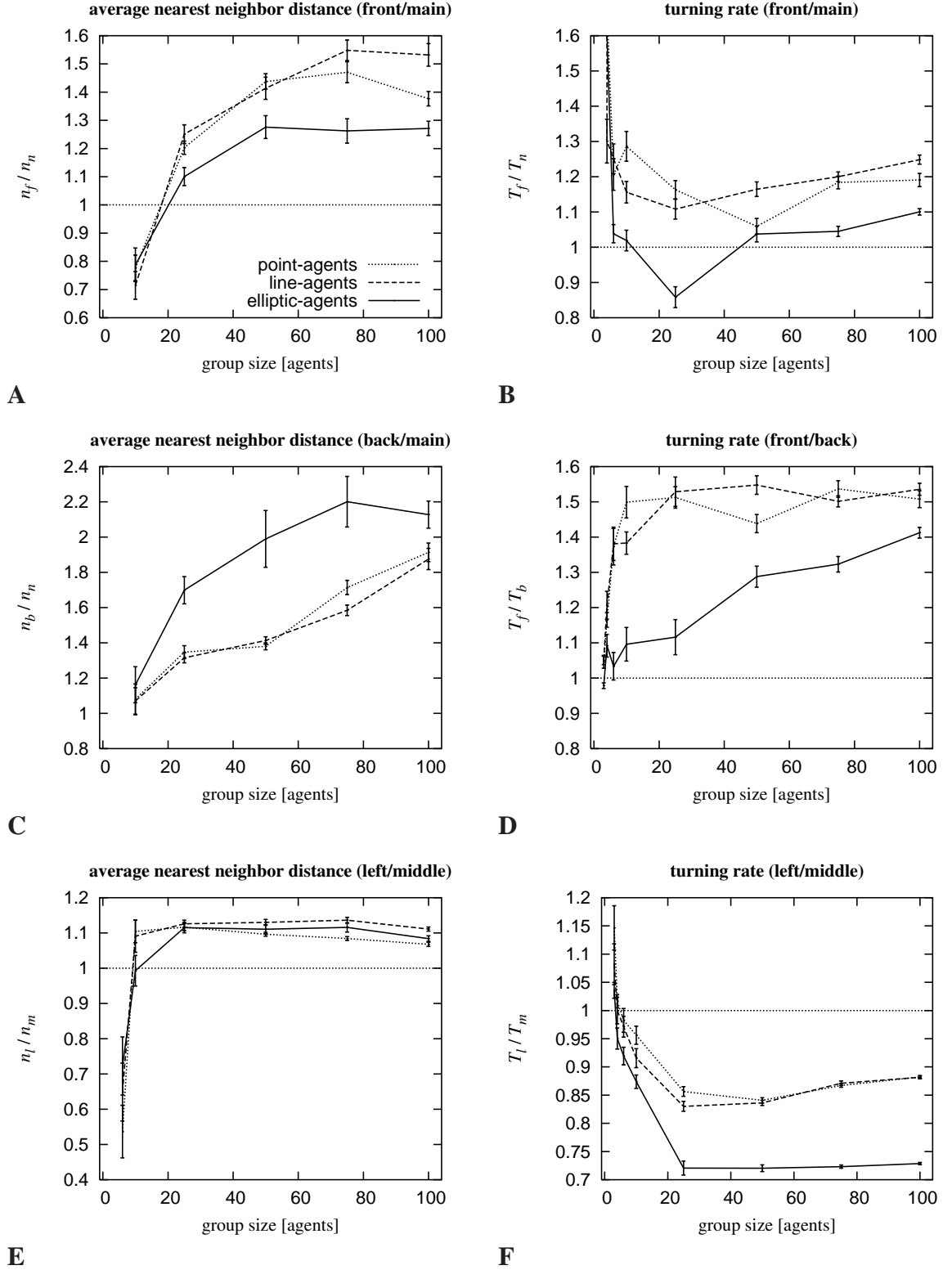
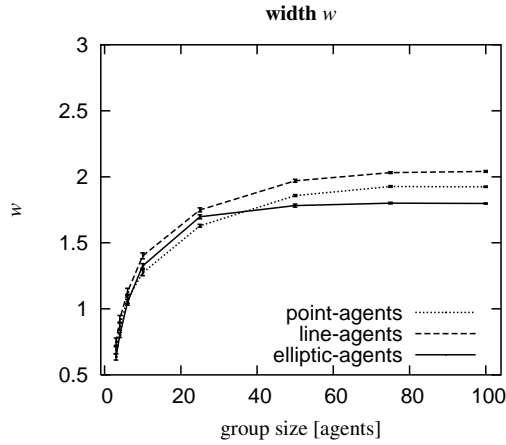
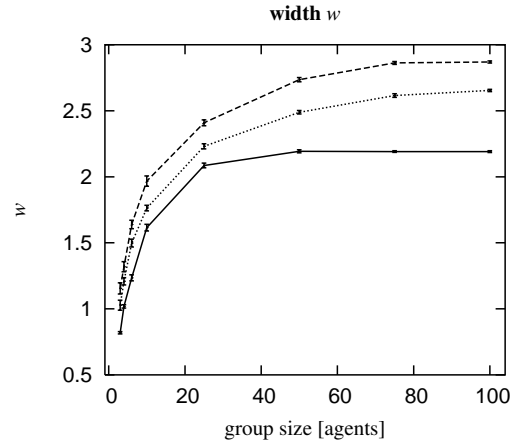
small agents ($b = 0.1\text{m}$)large agents ($b = 0.2\text{m}$)

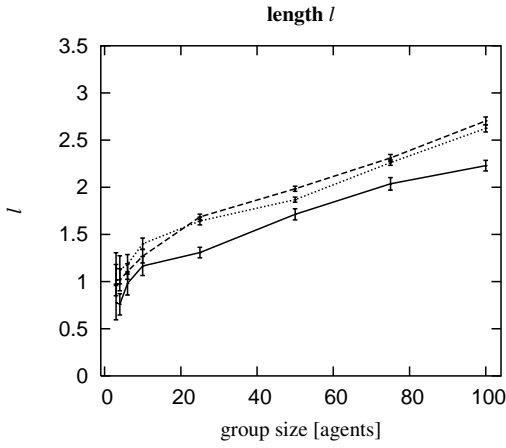
Figure 2.7 – Left Panels: Mean and S.E. of ratio of average nearest neighbor distances in different parts of groups of several group sizes consisting of small agents (the results for large agents are qualitatively similar). **Right Panels:** Mean and S.E. of ratio of average agent turning rates in different parts of the group for several group sizes of large agents (the results for small agents are qualitatively similar).

small agents ($b = 0.1\text{m}$)

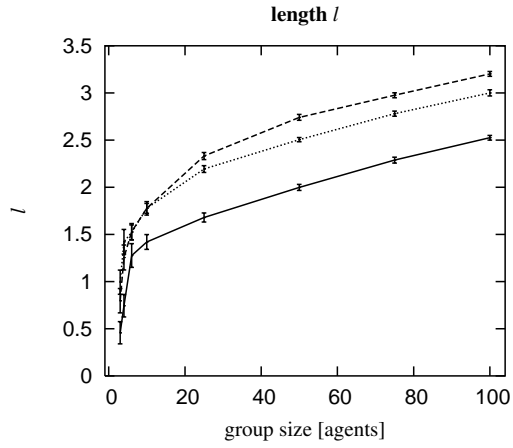
A

large agents ($b = 0.2\text{m}$)

B



C



D

Figure 2.8 – Average and standard error of group width and length for several group sizes of either small agents (left panels) or large ones (right panels). For definitions of width and length see Fig. 2.4.

lar, but confusion and, consequently, group speed differ in a different way among groups of line- and point-agents at the one hand and elliptic-agents, on the other hand. Groups of large line- (and point-) agents show less variation in heading direction, and therefore higher speed, than groups of small agents. However, for elliptic-agents, the reverse holds (Figs. 2.6A-D). Heading directions of point- and line-agents that are large are more coordinated than those among agents that are small due to the greater aligning area of larger agents (Fig. 2.1A). In contrast, among elliptic-agents the elliptic form of the repulsion area causes frequent turning. Because the repulsion area is lengthy, after turning away from certain group members, the individual soon finds others in its repulsion region and this provokes another repulsion reaction (Fig. 2.9). This “repeated-repulsion effect” is greater for large elliptic-agents than for small ones, because the form of their repulsion region is more asymmetric (Figs. 2.1B). In sum, groups of elliptic-agents (of both sizes) show greater confusion of heading directions than those of point- and line-agents due to the combined effects of the “repeated repulsion” and the smaller size of their

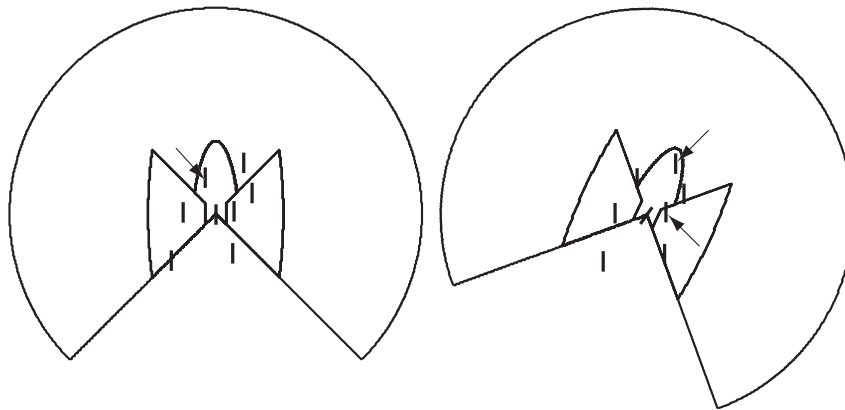


Figure 2.9 – *Effect of elliptic repulsion regions on agent behavior (“repeated repulsion effect”): The agent (center) avoids a close by agent (indicated by an arrow, left panel) by turning away (right panel). Because of the elliptic form of the repulsion region, other neighboring agents may be found in the repulsion region after the turn (indicated by arrows in the right panel), which will induce another avoidance movement in the next time step.*

aligning region (Figs. 2.1AB).

As regards group form, line-agents form the widest and longest groups, groups of point-agents are intermediate and those of elliptic-agents are smallest (Figs. 2.8A-D). The difference between line- and point-agents is due to the smaller body of point-agents. Groups of elliptic-agents, in turn, are smaller, due to their narrower repulsion area. Groups of large agents appear to be wider (Figs. 2.8AB) and more circular (data not shown) than those of small agents. This is possibly due to the fact that the attraction at the sides of the agents is weaker as a consequence of the greater aligning area. For all types, we find elongated schools (data not shown), at least at larger group sizes ($N > 50$).

2.4 Discussion

Our model, SchoolingWorld, shows several emergent phenomena: the number of agents in a group influences the group’s form, density, confusion, turning rate and group speed. Further, although all agents are completely identical, agent density varies depending on the specific location in the school (e.g. front or back). Besides, an elliptic body form leads to a more confused school and therefore, reduced group movement.

As regards the effects of group size, SchoolingWorld shows that larger groups have a higher agent density, are more confused and have a lower group speed. A larger expanse (which is similar to the average center distance) of larger groups, and, simultaneously, a decreased average nearest neighbor distance for larger groups, has also been found in former models (Huth and Wissel 1992; Reuter and Breckling 1994), but no explanation has been given for this phenomenon. Here, we explain such closer proximity to the average nearest neighbor (i.e. ‘huddling together’) by the stronger mutual attraction in larger groups due to the larger number of neighbors. Further, the increase in confusion (average deviation of the headings of the agents from the group average) in larger groups is in line with the findings of Reuter and Breckling (1994). It arises because in larger groups only a part of the agents directly aligns with each other (because of larger agent distance). For geometrical reasons, higher confusion lowers

group speed. The turning rate of larger groups in *SchoolingWorld* is slower due to the lower impact of the behavior of a single agent on the group and because there are more agents present to align with. This result contradicts part of the results by Romey (1996). Whereas he found that the speed of groups decreased in larger groups, simultaneously (in contrast to our results) group turning rate increased in larger (cohesive) groups. This difference may be attributed to the absence of aligning in his model. Therefore turning movements, which occur frequently in dense (large) groups because of repulsion, are not damped by aligning and thus may more easily lead to a change of direction of the whole group.

How do these effects of group size in *SchoolingWorld* relate to findings in real animals? Lower inter-individual distance in larger schools has been found in many fish studies (minnows: Partridge 1980; cod and saithe: Partridge et al. 1980). This makes it interesting to investigate confusion and group speed in relation to group size also. Such data would reveal whether our model captures the essentials of fish schooling. If confirmed, we may expect larger groups to fission more easily as a consequence of the increased confusion.

Although the agents are completely identical, they behave differently in different parts of the group. Average turning rate of agents is highest at the front. This arises, because agents at the front have no group members ahead of them and thus are attracted only to the partners at their sides. This causes the agents at the front to slow down and thus leads to a 'jam' near the front. Thus, in our model agents are distributed unevenly in the school. Density is higher in the center and at the front, and lowest at the back and therefore, the center of gravity is located in the front half of the school. Further, for larger group sizes, schools are usually longer than wide and this asymmetry increases with the number of agents. In our model these properties are emergent from the combination of attraction and aligning behavior due to which the agents are on average attracted to the center of the group while moving forwards.

A similar slowing-down and 'jamming' has been found by Deneubourg et al. (1989) in the model that closely resembles the swarming behavior of army ants. Further, exactly these school characteristics (of frontal density and oblong groups) have been found in shoals of roach (*Rutilus rutilus*) by Bumann, Krause, and Rubenstein (1997). Using models of predation minimization and corresponding experimental procedures on creek chub (*Semotilus atromaculatus*) the authors conclude that both, increased density in the front of the school and the elongated shape of groups, are a way to minimize the predation risk by hiding from the periphery and behind others (as suggested by the 'selfish herd theory', Hamilton 1971). The authors, however, do not offer any ideas on how individual fish may attain such characteristics of school form and heterogeneous density. *SchoolingWorld* suggests a solution: An oblong group-shape and the highest density at the front of the school may automatically result from the simple behavioral rules of repulsion, aligning, and attraction.

Note that even though we provided agents with a speed that is fixed (with random noise, as is also done in the other models Aoki 1982; Couzin et al. 2002; Huth and Wissel 1992) the front agents still appear to be 'slowing down' and effects of group structure and size closely resemble patterns that have been studied in fish so far. This minimal representation, thus, seems to suffice to reproduce these phenomena. On the other hand, adaptation of speed between neighboring agents is an interesting extension to study in future models.

As regards our preliminary representation of 'embodiment', we have compared the effect of two body sizes and of three body forms (point, line, and elliptic) on patterns of schooling for a range of different school sizes. As regards size of the agent, larger body size is accompanied by a larger area of repulsion and alignment and, therefore, nearest neighbor distance is larger

and coordination is stronger among large than small (point- and line, but not elliptic) agents. These results are in agreement with those by Olst and Hunter (1970) in their comparative study between adult and juvenile (instead of large and small) fish. Olst and Hunter, however, attribute lower cohesion and alignment to the higher feeding rates of juvenile fish, whereas in our model these differences are a direct consequence of body size, i.e. size of the region of repulsion and aligning.

Of the three body forms, groups of line-agents have, compared to those of point-agents, a slightly larger average center distance, they are wider, longer and less homogeneous; other school characteristics are similar. The greatest differences, however, are found between elliptic-agents and the others. Groups of elliptic-agents are more cohesive (in average center distance as well as nearest neighbor distance); they are less homogeneous, because the inter-individual distance of agents swimming side to side is much shorter than those swimming behind each other. Further, they show higher confusion and confusion is greater among large agents than small ones, whereas among point- and line-agents the reverse holds. These phenomena are directly related to the elliptic form of the repulsion region (which is more asymmetric for the large agents), which is associated with the “repeated repulsion effect”. Although intuitively, the representation of fish as an elliptic- agent seems more natural than that of point- or line-agent, this cannot be judged at present from the results. In this context, it is of interest to compare confusion among groups of small adult individuals and large ones of the same species: if confusion is greater among the larger individuals this provides support for the model of ‘elliptic’ agents as being a better representation than that of point- and line-agents. This is, of course, still a preliminary representation of the body and each level of detail that will be added (such as a body that can bend) in future, may lead to new hypotheses as regards collective phenomena in real fish. The main function of models like SchoolingWorld may be to provide us with useful new hypotheses.

Chapter 3

Density distribution and size sorting in fish schools: an individual-based model¹

Abstract

In fish schools the density varies per location and often individuals are sorted according to familiarity and/or body size. High density is considered advantageous for protection against predators and this sorting is believed to be advantageous not only to avoid predators but also for finding food. In this paper, we list a number of mechanisms and we study, with the help of an individual-based model of schooling agents, which spatial patterns may result from them. In our model, schooling is regulated by the following rules: avoiding those that are close by, aligning to those at intermediate distances, and moving towards others further off. Regarding kinship/familiarity, we study patterns that come about when agents actively choose to be close to related agents (i.e., ‘active sorting’). Regarding body size, we study what happens when agents merely differ in size but behave according to the usual schooling rules (‘size difference model’), when agents choose to be close to those of similar size, and when small agents avoid larger ones (‘risk avoidance’). Several spatial configurations result: during ‘active sorting’ familiar agents group together anywhere in the shoal, but agents of different size group concentrically, whereby the small agents occupy the center and the large ones the periphery (‘size difference model’ and ‘active sorting’). If small agents avoid the risk of being close to large ones, however, small agents end up at the periphery and large ones occupy the center (‘risk avoidance’). Spatial configurations are also influenced by the composition of the group, namely the percentage of agents of each type. Furthermore, schools are usually oblong and their density is always greatest near the front. We explain the way in which these patterns emerge and indicate how results of our model may guide the study of spatial patterns in real animals.

3.1 Introduction

In natural shoals of fish, the highest density is often at the front (Bumann, Krause, and Rubenstein 1997) and schools are usually oblong (Pitcher 1980). This is attributed to the tendency to seek protection against predators, as the front is regarded as the most dangerous part (Bumann,

¹appeared as C. K. Hemelrijk and H. Kunz (2005). „Density distribution and size sorting in fish schools: an individual-based model“. In: *Behav. Ecol.* 16.1, pp. 178–187

Krause, and Rubenstein 1997). Furthermore, it appears that individuals are assorted by familiarity (e.g., Barber and Ruxton 2000; Griffiths and Magurran 1999) and body size (Hoare et al. 2000; Krause, Godin, and Brown 1996; Krause et al. 2000; Peuhkuri, Ranta, and Seppä 1997; Svensson, Barber, and Forsgren 2000). Segregation by familiarity is thought to be beneficial because of cooperation against predators (Trivers 1971) because it allows cohesion (Chivers, Brown, and Smith 1995), and it is also supposed to have foraging advantages. Segregation by size may be beneficial for two reasons: it may facilitate coordination of movement (Theodorakis 1989), and it can have hydrodynamic advantages (Pitcher, Magurran, and Edwards 1985). Because fish of the same size are under the same selection pressure (Pitcher, Magurran, and Allan 1986) and have the same needs, they may synchronize their behavior; and by clustering together they may reduce their visual conspicuousness, via reduction of the so-called ‘oddity effect’ (Landeau and Terborgh 1986; Ranta, Peuhkuri, and Laurila 1994).

Small individuals are either found at the periphery of the school (Krause 1993b; Theodorakis 1989) or in the center (Romey 1997). There are descriptions of water insects in which small individuals remain in the center (Sih 1980) and of fish in which they are at the periphery (Krause 1993b). This may be related to different predator tactics; in insects predators often enter the swarm (Sivinski 1997), but in fish this is rare (Krause 1994a).

Here, we do not want to give a functional explanation in terms of what is best for the fitness of different categories of individuals, but we try to connect a number of behavioral rules and body characteristics on the one hand to spatial patterns at a group level (i.e., ‘macro-patterns’) on the other. This we do by means of an individual-oriented model of agents that school (called *SchoolingWorld*). We start from specific body characteristics and rules of behavior and are guided by the patterns that the model itself generates. We use the emergence of these patterns as hypotheses that may be investigated in real fish schools. This is a useful method, because complex patterns of behavior at a group level are more easily understood from the ‘bottom up’ than from the ‘top down’ (Braitenberg 1984; Hemelrijk 1996; Pfeifer and Scheier 1999).

3.2 Methods

3.2.1 Introduction to the model

Let us discuss mechanisms that may underlie spatial assortment by familiarity and size.

An ‘active’ preference to shoal with familiar individuals or with fish similar in size has been demonstrated in experiments several times: a single fish in a central compartment had the choice to swim close to a compartment containing fish of a similar or a different body size (Krause 1994b; Krause and Tegeder 1994; Ranta, Juvonen, and Peuhkuri 1992; Ranta, Lindström, and Peuhkuri 1992; Ward, Gobet, and Kendall 2001) and also close to a compartment with fish of different degrees of familiarity (e.g. Griffiths and Magurran 1999).

Furthermore, size assortment may be caused by differences in the swimming speed of fish of different sizes. Pitcher and Parrish (1993), however, say that this leads to complete separation of groups by size and, therefore, that it cannot explain size segregation in shoals. On the other hand, Couzin (2003) have shown in a model that individual differences in swimming speed may lead to segregation of individuals in the same school, if the agents adjust their speed to that of their neighbors. In this paper, we study other mechanisms that may lead to segregation by size.

Size assortment in schools may also be the result of aggression as described for sardines,

Engraulis japonicus (Kimura 1934), the Atlantic herring (Schäfer 1955), and cod (Brawn 1961). This may reflect competition for food or for mates. The effect of competition on spatial structure has been illustrated by Hemelrijk (2000) in a model called *DomWorld*. She shows that among artificial agents that group and compete in a virtual world, both a dominance hierarchy and a spatial structure develop. In this spatial structure agents are assorted by dominance rank with high-ranking agents in the center and low-ranking ones at the periphery. Because social dominance is often associated with a larger size (Myrberg Jr 1972; Thines and Heuts 1968), competition may also lead to assortment by size. We study this as a form of ‘risk avoidance’, meaning that small agents avoid large ones in order to avoid aggression from large ones, as described in (Pitcher, Magurran, and Allan 1986).

As a ‘control’ we investigate what happens if agents differ merely in size (without size-related rules of active assortment and without rules of risk avoidance).

To understand the patterns of segregation to which these conditions lead, we extend our earlier model *SchoolingWorld* (Kunz and Hemelrijk 2003) with characteristics of the agents (namely size and familiarity) and with behavioral rules for sorting and competition. This kind of model is useful because studies of complexity science have repeatedly shown that it is impossible to predict the consequences of individual behavioral rules at a group level without them (Camazine et al. 2001; Hemelrijk 2002b).

Our model *SchoolingWorld* has produced emergent (group-level) patterns that resemble those of schools of real fish (Kunz and Hemelrijk 2003). It is inspired by models of Huth and Wissel (1992, 1994b), Reuter and Breckling (1994) and Niwa (1994). In these models, schooling is a consequence of the tendency to avoid other fish that are close by, to align to those at intermediate distances, and to move towards others that are further off (but within the range of vision).

In the models designed by others, agents are represented as points with their sensory regions as concentric circles around them (here indicated as ‘point-agents’). In *SchoolingWorld*, we use a representation that is more realistic in two respects. First, the body is reflected as a line segment. Second, the sensory regions of repulsion and aligning are represented as ellipses (called ‘elliptic-agents’, see Kunz and Hemelrijk 2003), because they are situated (besides in the visual system) in the ‘lateral line system’ in real fish (Partridge and Pitcher 1980). The lateral line consists of a series of hydrodynamic sensors along both sides of the body (Bleckman 1993) that detect stimuli (e.g., changes in water pressure) close by. Therefore, ellipses reflect the operational area of the lateral line system more accurately than circles. We keep the region of attraction circular, however, because it is determined by vision (Partridge and Pitcher 1980).

To represent familiarity, we divide agents into two classes, familiar and unfamiliar. Whether individuals distinguish between these categories on the basis of smell or of visual appearance does not matter for the model. To represent two different body sizes (large and small), we vary the length of the line segment and the size of the sensory regions of repulsion and aligning. For ‘active sorting by size/familiarity’ we increase the attraction and aligning tendency of the agents and diminish their tendency to avoid others of similar size/familiarity compared to those of different size/familiarity. Note that ‘active sorting by familiarity’ is studied among agents of the same size. ‘Risk avoidance’ is implemented by supplying small agents with a strong tendency to avoid large agents. We compare collective patterns to those that result only from the effects of the difference in size (the ‘size difference’ model). Thus, any pattern that arises in the ‘size difference’ model emerges exclusively from body characteristics, whereas in the model of ‘risk assortment by size’ and ‘active avoidance’ patterns emerge from the combined

Parameter	Symbol and value
Time step	$\Delta t = 0.2\text{s}$
Speed (average and SD)	$v_{\text{avg}} = 0.3\text{m/s}$, $v_{\text{sd}} = 0.03\text{m/s}$
SD of the heading	$\alpha_{\text{sd}} = \frac{\pi}{72}\text{rad} \approx 2.5^\circ$
Turning rate, ‘default’	$\omega^{\text{def}} = \frac{1}{2}\pi\text{rad/s}$
Blind field in the back	$\gamma = 60^\circ$
Blind field for aligning region (front)	$\gamma' = 60^\circ$
Line length	small: $b = 0.1\text{m}$ large: $b = 0.2\text{m}$
Scaling factor of repulsion(3.8)	small: $a_r = 1.0$ large: $a_r = 2.0$
Scaling factor of attraction(3.9)	$a_a = 1.0$
Scaling factor of aligning(3.10)	$a_p = 1.0$
Ranges of repulsion(3.8)	small: $r_r = 0.3\text{m}$ large: $r_r = 0.6\text{m}$
Ranges of aligning(3.10)	small: $r_p = 1.0\text{m}$ large: $r_p = 2.0\text{m}$
Range of attraction	$r_a = 5.0\text{m}$
Eccentricity	small: $e = 2.0$ large: $e = 4.0$
‘Active sorting’	$c_r = 2.0$, $c_a = 2.0$, $c_p = 2.0$
‘Risk avoidance’	$c_{\text{riskAvoid}} = 20.0$ (varied from 0 to 40.0)

Table 3.1 – *Parameters of the agents.*

effects of size and the additional behavioral rules.

We characterize collective patterns by the spatial variation in density and by the spatial distribution of the two classes of agents (size/familiarity), by their degree of segregation, by the surface, and by the form of the school as a whole.

3.2.2 The model

SchoolingWorld is implemented in the programming language C. In addition, Octave², a high-level language intended for numerical (matrix) computations, was used for data post-processing and Gnuplot³, a command-driven interactive function-plotting program, to generate various types of graphs.

Fish schools have been modeled in 2-D as well as in 3-D. Comparing a particular 2-D model (Huth and Wissel 1992) to a 3-D one (Huth and Wissel 1994b), no additional phenomena are visible in the 3D-model. Therefore, we decided to implement our model, SchoolingWorld, in 2-D. The modeled artificial world is continuous and homogeneous. Time proceeds in discrete steps t . At each time step all agents are activated in random order.

²www.octave.com

³www.gnuplot.info

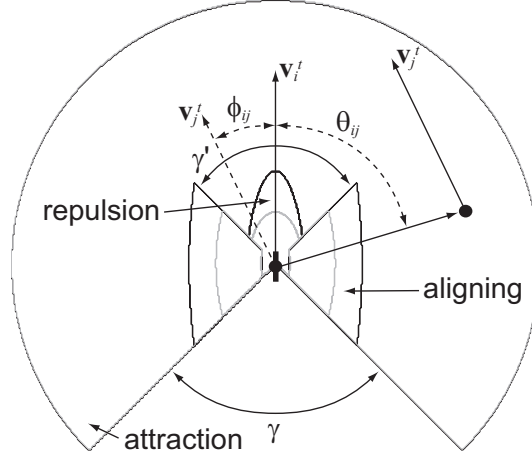


Figure 3.1 – The sensory regions of an agent. The agent is located at the center. The outermost circle represents the visual range, r_a . It contains three functional areas: of attraction, of aligning, and of repulsion (gray: regions of attraction and repulsion of small agents, black: the same of large ones).

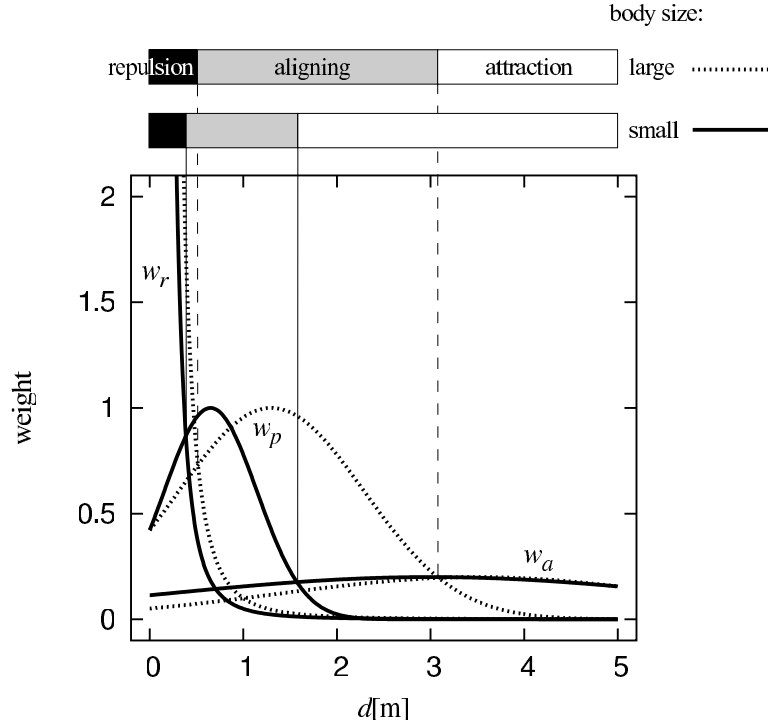


Figure 3.2 – Weight factors of repulsion, $w_r(d)$, attraction, $w_a(d)$, and aligning, $w_p(d)$, for small agents (solid lines) and large ones (dotted lines). d denotes the distance to the neighbor. Regions are classified into repulsion, aligning, and attraction by the largest of the three weight factors (top of figure). For further information, see text.

Position, speed, and heading

At the beginning of the simulation, a certain number of agents are put randomly in a starting area of $2.5 \times 2.5\text{m}$ and are given a random orientation, which was chosen between 0 and 90 degrees in order to obtain a single school. The initial speed of the agents was set to v_{avg} (see Tab. 3.1). At time t agent i is located at position \mathbf{x}_i^t and moves with a velocity \mathbf{v}_i^t (speed and direction) during one simulation step Δt .

$$\mathbf{x}_i^t = \mathbf{x}_i^{t-\Delta t} + \mathbf{v}_i^t \Delta t \quad (3.1)$$

Similar to models by others (see Aoki 1982; Couzin et al. 2002; Huth and Wissel 1992, 1994b), the speed of agents v_i^t does not depend on that of other agents but is an independent stochastic variable. It is drawn from a Gaussian probability distribution $P(v_{\text{avg}}, v_{\text{sd}})$ at each time step.

The agent's heading direction, α_i^t , is updated every simulation step as follows:

$$\alpha_i^t = P(\underbrace{\alpha_i^{t-\Delta t} + \omega_i^t \Delta t}_{\alpha_{i,\text{avg}}^t}, \alpha_{\text{sd}}) \quad (3.2)$$

whereby $\alpha_i^{t-\Delta t}$ is the agent's heading in the previous time step and ω_i^t its rate of turning or rotation (which depends on other agents, see next section). α_i^t is drawn from a Gaussian distribution with a variable mean, $\alpha_{i,\text{avg}}^t$, and fixed SD, α_{sd} . The heading, α_i^t , and the speed, v_i^t , constitute the velocity

$$\mathbf{v}_i^t = \begin{pmatrix} v_i^t \cos \alpha_i^t \\ v_i^t \sin \alpha_i^t \end{pmatrix} \quad (3.3)$$

Repulsion, attraction, and aligning

The artificial fish have three behavioral responses: repulsion (between agents at short distances), aligning (at intermediate distances), and attraction (at greater distances, see Breder Jr. 1954; Huth and Wissel 1992, 1994b; Warburton and Lazarus 1991).

Repulsion in nature is presumably determined by both the sensors of the lateral line and the visual system, and, therefore, we implement it as if it operates in an area immediately surrounding the agent, except for a 'blind area' at its back (Fig. 3.1). For aligning, the lateral line is most effective. Because it operates mainly at the sides, there are two 'blind areas' for aligning, one at the back and one at the front. Because attraction is determined by vision, there is only one 'blind area', at the back.

During repulsion an agent i turns away from a nearby agent j with rate of rotation (i.e., speed of turning)

$$\omega_r = \begin{cases} -\omega^{\text{def}} & \text{if } \theta_{ij}^t > 0 \\ +\omega^{\text{def}} & \text{otherwise} \end{cases} \quad (3.4)$$

where $\theta_{ij}^t = \angle(\mathbf{x}_j^t - \mathbf{x}_i^t, \mathbf{v}_i^t)$ (see Fig. 3.2) and ω^{def} is the 'standard' rate of rotation of the agents (see Tab. 3.1). Attraction implies that an agent i turns towards an agent j with a rate of rotation

$$\omega_a = \omega^{\text{def}} \theta_{ij}^t \quad (3.5)$$

Note that, in contrast to repulsion, rate of turning ω_a caused by attraction is proportional to θ_{ij}^t . Aligning implies that agent i matches its orientation to that of agent j by turning with rate of rotation

$$\omega_p = \omega^{\text{def}} \phi_{ij}^t \quad (3.6)$$

where $\phi_{ij}^t = \angle(\mathbf{v}_j^t, \mathbf{v}_i^t)$ is the difference in the heading direction of the two agents (see Fig. 3.2). The actual behavioral reaction depends on the weights of repulsion (w_r), attraction (w_a), and aligning (w_p). These weights depend on the distance to the other agent (as in Reuter and Breckling 1994), as follows:

$$d_{ij} = \|\mathbf{x}_j - \mathbf{x}_i\| \quad (3.7)$$

$$w_r(d) = \min\left(\frac{0.05a_r}{d^3}, 10\right) \quad (3.8)$$

$$w_a(d) = 0.2a_a e^{-\left(\frac{d - \frac{1}{2}(r_a + r_p)}{r_a - r_p}\right)^2} \quad (3.9)$$

$$w_p(d) = a_p e^{-\left(\frac{d - \frac{1}{2}(r_p + r_r)}{r_p - r_r}\right)^2} \quad (3.10)$$

The behavioral reaction is calculated as the weighed sum,

$$\omega_{ij}^t = w_r(d_{ij}^t)\omega_r + w_a(d_{ij}^t)\omega_a + w_p(d_{ij}^t)\omega_p \quad (3.11)$$

The dependence of the weight factors on the distance d_{ij}^t to the interaction partner makes behavioral transitions continuous instead of discrete. Nevertheless, for convenience, we name the three behavioral regions (Fig. 3.1) after the weight factor with the largest value (Fig. 3.2).

When agent i perceives more than one agent j , its behavioral response (turning rate) is calculated as the average of its response to each neighbor separately.

Body representation

We represent both the size and the form of the agent's body in so-called 'elliptic' agents (Fig. 3.1); the body is represented by a line segment (with variable length, b , Tab. 3.1), and regions of repulsion and of aligning are elliptic, reflecting the operational area of the lateral line system (Healey and Prieston 1973), whereas that of attraction is circular, reflecting the range of vision (for construction details see Kunz and Hemelrijk 2003).

We represent the agent's size (large or small) by the length of the line b and by the size of the regions of repulsion and aligning (the size of the region of attraction is kept independent of body size because it reflects the area of vision). In line with the findings by Olst and Hunter (1970) that inter-individual distance increases with body size, but less so than proportionally to body length, we increase the size of the repulsion and aligning regions accordingly (by scaling a_r , r_r , and r_p ; Figs. 3.1 and 3.2, Tab. 3.1, Equations (3.8), (3.9), (3.10)). Furthermore, because the increase in length of larger fish is greater than its increase in width, we made the asymmetry of the elliptic regions of large agents greater than that of small ones (see 'eccentricity', e , Tab. 3.1). Note that by using a line (instead of a point) to represent the agent's body, it occupies space and others often perceive it as being slightly closer than if it is represented as a point (Kunz and Hemelrijk 2003).

'Active sorting' and 'risk avoidance'

In the case of 'active sorting' we lower the tendency to avoid agents of similar size (or familiar agents) and increase the tendency to avoid others of different size (or that are unfamiliar), by dividing/multiplying the scaling factor of repulsion, a_r , by a constant, c_r (see Tab. 3.1). In addition, the strength of aligning and attraction among fish of the same size (or that are familiar)

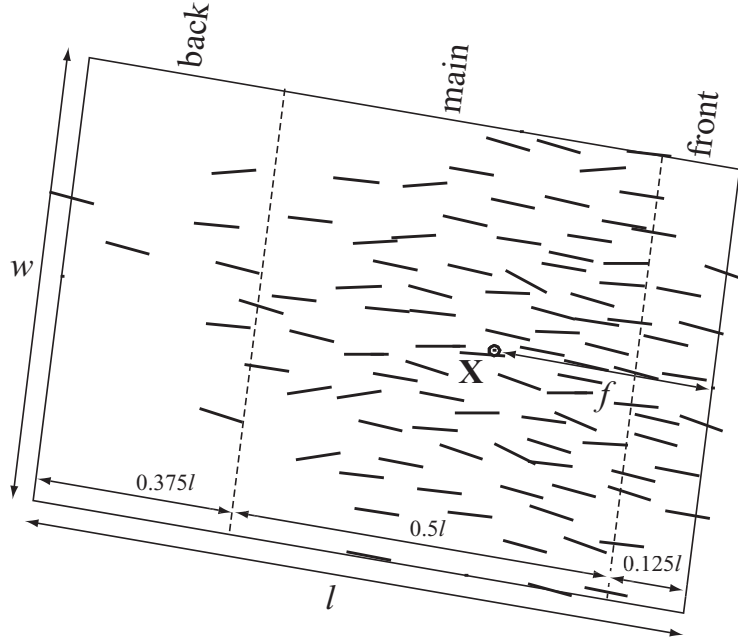


Figure 3.3 – The method for obtaining measures of group width (w), length (l), and distance to front (f). The snapshot is randomly chosen and indicates the positions and orientations of agents in different parts of the school (front, main, and back).

is increased, whereas it is reduced among individuals of different size (or that are unfamiliar). We implemented this by multiplying/dividing the scaling factor of aligning, a_p , by a constant, c_p , and that of attraction, a_a , by a constant, c_a .

‘Risk avoidance’ is asymmetric. The tendency of small agents to avoid large ones is increased, but the tendency of large ones to avoid small ones is not changed. This is realized by the scaling factor of repulsion, a_r . During an encounter of a small fish with a large one, it is multiplied by a constant, $c_{\text{riskAvoid}}$. This can be interpreted as the avoidance of a potential danger by small fish.

3.2.3 Data and measures

We study each model (familiarity assortment, size difference, risk avoidance, and active assortment) for different percentages of each type (small and large) of agent (0%, 25%, 50%, 100%). Groups always consisted of 100 agents. We performed 25 runs for each combination.

For each simulation step the following statistics are calculated. As an indication of the expanse of the group (compare ‘expanse’ by Huth and Wissel 1992), we use the average distance of all agents to the center of the school, c^t :

$$c^t = \frac{1}{N} \sum_i \| \mathbf{X}^t - \mathbf{x}_i^t \|, \quad \mathbf{X}^t = \frac{1}{N} \sum_i \mathbf{x}_i^t$$

where \mathbf{X}^t denotes the center of the school (center of gravity, calculated as the average x - and y -values over all agents). N indicates the number of agents.

The so-called ‘normalized center distance of large agents’ characterizes the spatial configuration of small and large agents in the school. It is the average distance of the large agents to

the center of gravity, c_l^t , divided by the average distance of all agents to the center of gravity, c_t :

$$c_l^t = \frac{1}{c_t} \frac{1}{N_l} \sum_i \|\mathbf{X}^t - \mathbf{x}_i^t\|$$

N_l denotes the number of large agents. If c_l^t is greater than one, large agents are more likely to be found at the periphery, whereas if it is less than one, they tend to occupy more central positions.

To quantify the coordination of the heading directions of the agents, we measure the deviation of each agent's orientation to the average heading, α_{avg}^t , of the group. This is usually referred to as 'polarization', p^t (Huth and Wissel 1992), but we call it 'confusion', because higher values indicate greater disorder (Kunz and Hemelrijk 2003). It is calculated as the square root of the mean quadratic deviation angle:

$$p^t = \sqrt{\frac{1}{N} \sum_i (\alpha_{\text{avg}}^t - \alpha_i^t)^2}, \quad \alpha_{\text{avg}}^t = \angle \left(\frac{1}{N} \sum_i \mathbf{v}_i^t \right)$$

To quantify the form of the school, we enclose the complete school by the smallest rectangle oriented parallel to the direction of movement of the group (Fig. 3.3) and we calculate the degree to which a group is oblong, by dividing group width (orthogonal to the swimming direction) by group length (the longest group size in the direction of swimming).

To indicate the degree of centrality of the position of the center of gravity, \mathbf{X}^t , we divide the distance of the center of gravity to the front by the total length of the group.

To detect variation in turning rate depending on location, we calculate the average agent turning rate (i.e., the absolute rate of change of the agent's heading direction) in the front, main, and back section of the group separately (Fig. 3.3).

Group speed v_g^t is measured as the speed of the center of gravity, \mathbf{X}^t , of the group. Per run these measures were averaged over time steps 2000-3000 (omitting the transitory period). Averages and their SEs over 25 runs are plotted in Figs. 3.4 and 3.5. We discuss only results that are clearly significant, which can be judged from the large differences between the average values and the small sizes of the SEs. Furthermore, we confine ourselves to runs in which agents aggregate in a single school (as happened in 98.9% of the runs) that is polarized and coordinated (Shaw 1970), because in real fish size assortment is mainly found in such schools (Krause 1994b; Krause and Tegeder 1994).

3.3 Results

3.3.1 Density and form of schools

For all behavioral mechanisms and group compositions, the density of the agents is higher at the frontal part of the school. This is measured by the relative position of the center of the school (i.e., distance of the center of gravity to the front divided by the total length of the school is smaller than 0.5; see Fig. 3.4A). This is due to several causes: at the very front individuals align and are attracted to neighbors at their sides only (there are no or only few neighbors ahead). Consequently, the turning rate of agents is higher at the front than in the main part of the school (Fig. 3.4B). This slows down the forward movement of frontal agents (as they zigzag instead of moving straight) and a 'jam' develops near the front.

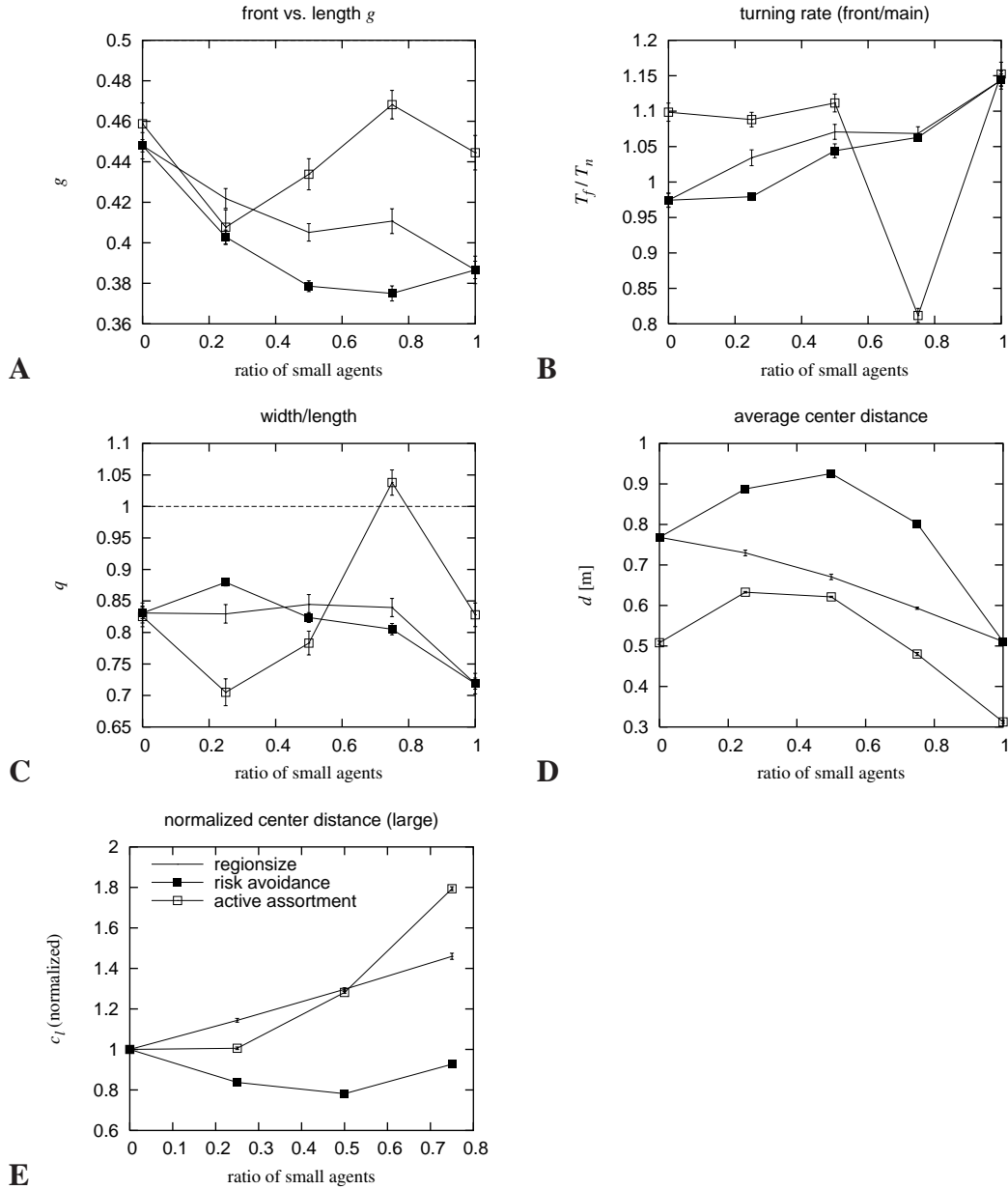


Figure 3.4 – Averages and SE of various measurements for models of ‘body size’, ‘active assessment’, and ‘risk avoidance and for different percentages of small agents. **A:** Location of the center of gravity. **B:** Turning rate among agents at the front divided by that among agents in the middle of the school. **C:** Degree to which groups are oblong. **D:** Average distance to center. **E:** Normalized average center distance of large agents.

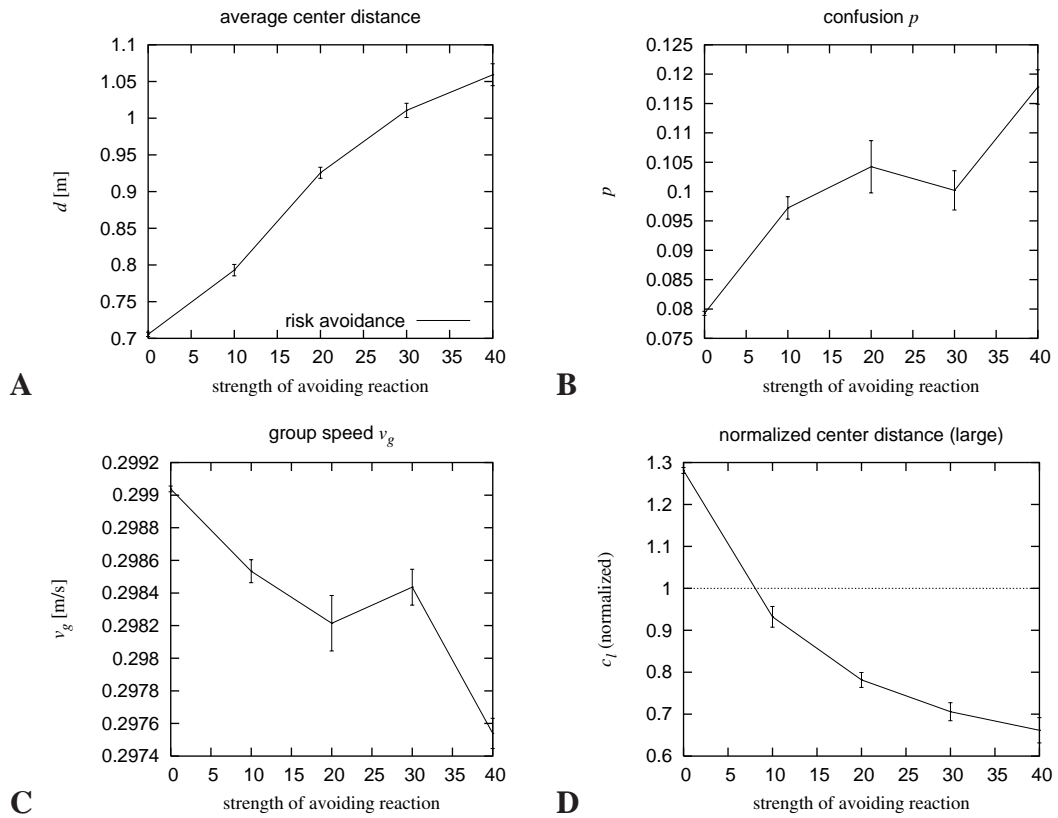


Figure 3.5 – Degree of ‘risk avoidance’ of (A) group surface, (B) confusion, (C) velocity of the group, and (D) (normalized) center distance of large agents (average and SE). Groups contain an equal number of small and large agents.

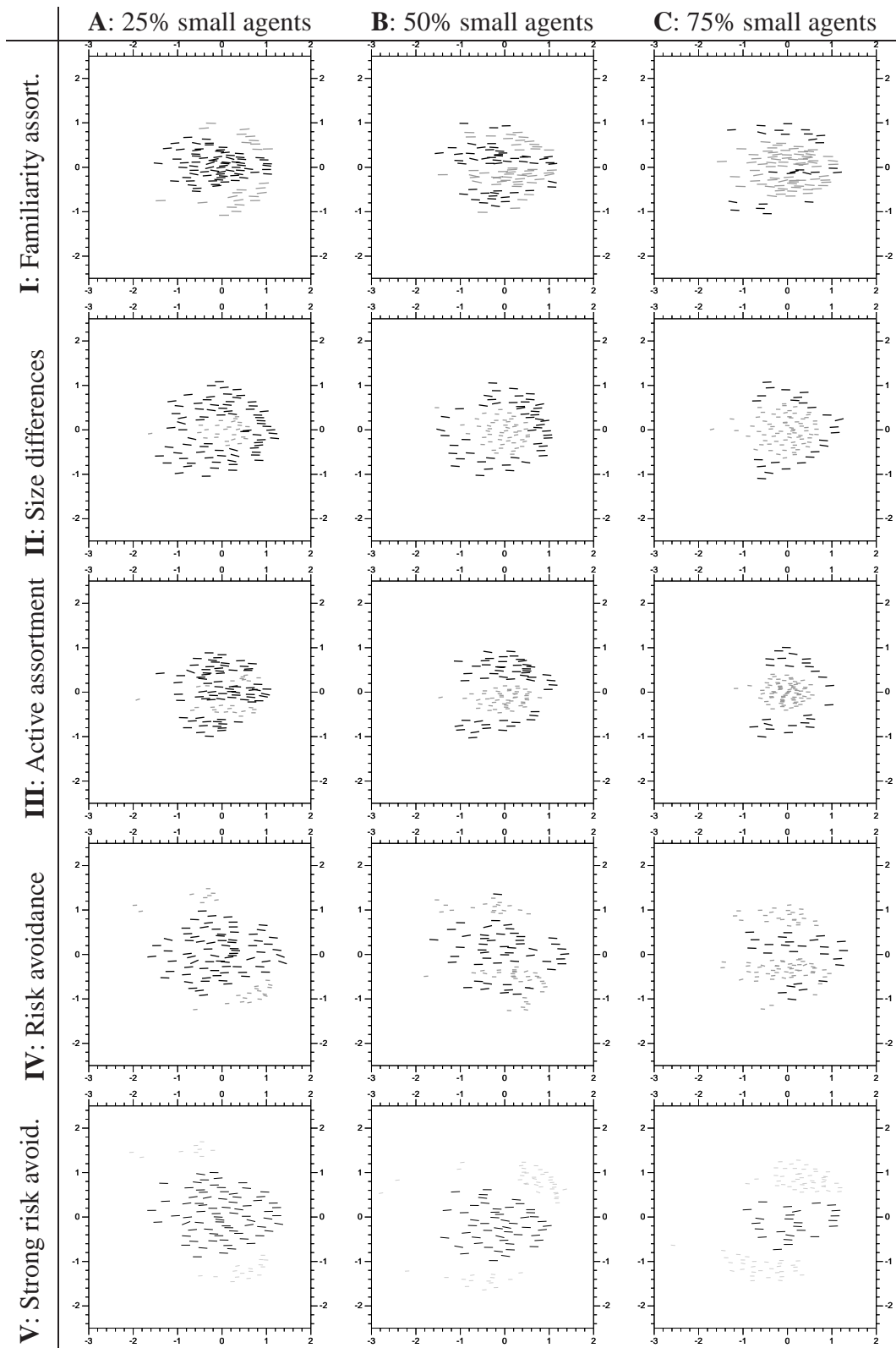


Figure 3.6 – End configuration of single runs (randomly chosen) of different models with different percentages of small agents. Light gray: small agents, dark: large agents. (V) Strength of risk avoidance is doubled. For further explanation see text.

The form of the school is usually oblong (group width divided by length being smaller than one; see Fig. 3.4C), because individuals approach each other from the side only (by turning towards each other) and not from the back (because they cannot speed up). An exception is that during ‘active sorting’ in a school with many small agents (75%), the group is slightly wider than long (Fig. 3.4C). This is caused by the clustering of a subgroup of large agents at each side of the school (Fig. 3.6IIC).

Groups are most compact (as measured by the average distance of all agents to the center) during ‘active size assortment’ and least compact during ‘risk avoidance’ (Fig. 3.4D). This is because ‘risk avoidance’ causes small agents to maintain a larger distance to large ones and, therefore, the group spreads out. Increasing ‘risk avoidance’ (from $c_{\text{riskAvoid}} = 0$ to 40) enlarges the surface or expanse of the group (measured by the average center distance), decreases its coordination (increases confusion), and, therefore, slows it down because of more frequent zigzag movements (Fig. 3.5A, B, and C, respectively).

3.3.2 Segregation by familiarity and by size

Assortment according to familiarity among agents of the same size leads to subgroups of familiar agents that may occur at any location in the group (Fig. 3.6I). Segregation is clearer if one class of agents is in the minority (25%). This arises because cluster formation by attraction among only a few agents tends to lead to a single cluster only. More agents (50%) can form several clusters (Fig. 3.6IB).

Assortment according to size is, in contrast to assortment according to familiarity, a concentric configuration. In the models of ‘active sorting’ and ‘size differences’ large agents occupy the periphery and small ones the center (Fig. 3.6II, III), and this pattern is reversed in that of ‘risk avoidance’ (Fig. 3.6IV and 3.6V).

Remarkably, also in the model of ‘size difference’ that lacks a preference for similar agents, spatial assortment is found. This is a consequence of the difference in size between agents, which drives large agents to the periphery, because their larger repulsion regions cause them to avoid small ones at a greater distance than vice versa (Fig. 3.6II).

In contrast to ‘active assortment by familiarity’, ‘active assortment by size’ leads to a concentric spatial configuration of agents of both sizes. This arises from the additional effect of size difference. Note that during ‘active assortment by size’ the segregation is stronger than in the ‘size difference’ only model, because it is supported by a preference to keep agents of similar size in close proximity (compare Fig. 3.6III and II).

‘Risk avoidance’, in contrast, counteracts the effects of ‘size difference’, because by strongly avoiding large agents, small agents avoid large neighbors earlier than vice versa, and consequently the small ones are driven to the periphery. Thus, the spatial configuration may reverse (Fig. 3.6IV). Obviously, whether or not this spatial reversal actually occurs during ‘risk avoidance’ depends on the relative strength of risk avoidance (represented by $c_{\text{riskAvoid}}$). The stronger it is, the clearer the reversed spatial configuration with small agents at the periphery and large ones in the center becomes (Fig. 3.6V). The center distance of large agents thus becomes increasingly smaller than one while increasing ‘risk avoidance’ ($c_{\text{riskAvoid}}$ from 0 to 40; see Fig. 3.5A). Lower values (less than one) indicate that large agents are closer to the center and small ones to the periphery (as shown for the highest degree of risk avoidance [$c_{\text{riskAvoid}} = 40$] in Fig. 3.6V for different group compositions). Due to the small body size, and thus closer proximity of small agents, more than 50% of small agents are needed to surround the large ones

completely (Fig. 3.6V).

There are two deviations from these spatial patterns. When large agents are at the periphery, they sometimes are lacking at the back (Fig. 3.6IIC, IIIB, IIIC) and when small agents are on the outside (during ‘risk avoidance’), segregation is weak (Fig. 3.6IVB, IVC). Large agents are lacking at the back because they move to the side to avoid having small ones directly ahead of them. In the ‘size differences’ model, this happens mainly when the number of large agents is small (Fig. 3.6IIC), but during ‘active sorting’ it also takes place when large agents and small ones are equal in number (Fig. 3.6IIIB, IIIC), because large agents are attracted by other large ones to the periphery, in addition to just avoiding small ones ahead of them.

Furthermore, segregation is weak if the percentage of agents that have a more extensive tendency to avoid others is large. Thus, during ‘active sorting’, if large agents are numerous (and small agents are few, 25%), they will form several clusters, because they easily find each other. These clusters are stable because large agents that are at their borders avoid small ones and thus move back into the cluster. Thus, these clusters remain stuck among small agents, preventing further segregation (i.e., joining of clusters).

Thus, during ‘risk avoidance’ segregation is weak for medium and high percentages of small agents due to similar cluster formation because small agents get stuck among large ones (Fig. 3.6IVB, IVC). In contrast, when the percentage of small agents is low, they have little opportunity to cluster together (because they seldom meet each other) and thus are driven to the periphery (Fig. 3.6IVA).

The typical spatial configuration, with large agents at the periphery (in the cases of ‘size difference’ and ‘active sorting’) and small agents at the periphery (in the case of ‘risk avoidance’), differ significantly from each other, as can be seen from the (normalized) center distance, c_l , of large agents shown in Fig. 3.4E. Note that values less than one indicate that large agents are in the center, and those greater than one indicate that large agents are at the periphery.

In the cases of ‘size difference’ and ‘active sorting’, where the small agents occupy the center, the average center distance of large agents increases with the percentage of small ones: a larger number of small agents naturally take up a larger area. Thus, the large agents, which are located peripherally, are further from the center (see Fig. 3.4E). Note that during ‘active sorting’ at a low percentage of 25% small agents, the average normalized center distance of large agents, c_l , equals approximately one, and thus small agents are not clearly in the center because they get stuck among large ones as mentioned above (see Fig. 3.6IIIA).

Conversely, in the case of ‘risk avoidance’, where the large agents are found in the center, a small number of large agents occupies a smaller surface, and this decreases the average distance to the center of larger agents, c_l . At 25% large agents (75% of small ones), there is an increase in the center distance of large agents despite their low number, because clusters of small agents, as mentioned above, may be caught in-between large agents and thus may stay in the center (see Fig. 3.6IVC).

3.4 Discussion

SchoolingWorld generates a wide range of spatial patterns. For instance, the center of the school (center of gravity) is located in the front half of the school and schools are oblong; sorting according to familiarity causes familiar agents to cluster at any place in the group; agents of different size sort themselves concentrically, with large agents in the center and small ones at

the periphery or vice versa.

3.4.1 Density and form of schools

In the model, the density in the school is highest near the front: the center of gravity is always located in the front half. This arises by self-organization as follows.

Because agents at the front see no group members ahead of them, they are attracted only by those at either side. Therefore, their movement direction varies continuously (their turning rate is high), which causes them to slow their forward movement. Note that even though we provide agents with a fixed velocity (with random ‘noise’, as is the case in the other models (Aoki 1982; Couzin et al. 2002; Huth and Wissel 1992, 1994b)), the front agents still appear to be ‘slowing down’ because of their zigzag movement. This leads to a ‘jam’ near the front.

Schools are usually oblong. In an earlier model (Kunz and Hemelrijk 2003) we found that this oblong form also occurs in schools of agents of one size and that it becomes more marked with a higher number of agents. This arises in the model from the combination of aligning behavior and the overall attraction of the agents to the center of the group. This attraction causes the agents to turn towards the center and consequently reduces the width of the group. Because the agents move forward at a ‘constant’ speed, the ones that lag behind cannot accelerate, and therefore the length of the group remains constant.

Remarkably, a similar slowing-down and ‘jamming’ has been found by Deneubourg et al. (1989) in a model that closely resembles the swarming behavior of army ants. Exactly the same characteristics (of frontal density and oblong groups) have also been found in shoals of roach (*Rutilus rutilus*) by Bumann, Krause, and Rubenstein (1997).

Using models for minimization of predation and corresponding experimental procedures on creek chub (*Semotilus atromaculatus*), these authors conclude that both traits are beneficial to minimize predation risk. Bumann, Krause, and Rubenstein (1997), however, do not provide a theory to explain how fish come to form such characteristic schools. SchoolingWorld does suggest an explanation: an oblong group-shape with the highest density at the front automatically results from the behavioral rules of repulsion, aligning, and attraction. It is of interest to verify the origin of the high density at the front in schools of real fish by analyzing whether the turning rate is higher at the front than in the main part of the school.

3.4.2 Spatial segregation by familiarity and size

Segregation by familiarity (in the absence of size differences) is clearer if one class of agents is in the minority. This arises because in this case there are fewer agents to be attracted to and, therefore, clusters become fewer, but larger. A similar result has been found by Schelling (1971) in his model of racial segregation, in which two types of agents require at least a minimum percentage of agents of the same type close by, otherwise they leave the subgroup. Stronger clustering of individuals whose type is in the minority is adaptive in nature, because fish of the minority type run a higher risk of predation, as Theodorakis (1989) has shown in his experiments in which odd-sized fish were eaten more often by large mouth bass, *Micropterus salmonides*. SchoolingWorld and Schelling’s (1971) model show that such stronger clustering may arise as an emergent phenomenon.

In the ‘size difference’ model (in which agents merely differ in body size), size sorting is spatial and emerges purely from the larger repulsion region of large agents. This provides us

with yet another reason why large agents may be at the outside of the group: their large size.

Our results are supported by those of related models used by Romey (1996) and Couzin et al. (2002); in shoals in which the repulsion area of the agents differed, agents with smaller repulsion areas appeared to end up in the center. (Note that here we also varied the size of the line segment and the aligning area.)

The mechanism of ‘active assortment by size’ strengthens segregation according to body size via self-reinforcing effects. The larger the cluster of identical agents, the stronger the attraction of other agents of the same size. Similar effects are found for clustering of all kinds of objects and organisms (Camazine et al. 2001; Schelling 1969). However, the pattern of small agents in the center is disturbed when the percentages of large and small agents differ; if large agents are in the majority (75%), clusters of large agents tend to get stuck among small ones. If large agents are rare, they cluster together at the side, because they avoid small ones ahead of them.

Furthermore, the degree of segregation during ‘risk avoidance’ is higher when small agents are few, because then large agents are in the center surrounded by separate clusters of small ones. If, however, small agents are numerous, they find each other more easily and end up in clusters that are trapped among large agents. The degree of segregation depends on the strength of the tendency of ‘risk avoidance’, since it is counteracted by effects due to differences in size; large agents move to the periphery because their repulsion area is larger, but ‘risk avoidance’ reverses the situation if small agents have an even stronger tendency to avoid large ones than vice versa. In DomWorld (Hemelrijk 1998, 2000), in contrast, such counteracting forces are absent during the process of dominance assortment, because here all agents have identical sensory regions. Agents differ only in their capacity to win or lose fights. Subordinates that lose more often flee more frequently and, therefore, automatically end up at the periphery of the group.

3.4.3 Spatial segregation in real fish

Of course, our model is no more than a minimal representation of what happens in real fish. In real fish body size varies continuously and real fish of different body size differ in many more aspects than we have studied here. For instance, they may differ in their tail-beat and swimming speed. These two traits may augment assortment even further than is the case in our ‘size difference’ model. Also, our model does not represent food and feeding behavior, and the distribution of food, of course, influences the distribution of individuals. If food is clumped, large individuals that are hungry will drive smaller ones to the periphery. If food is distributed randomly, most food is obtained at the periphery of the group.

Both spatial distributions found in the model, with large agents at the periphery or in the center of the group, are found in nature. The spatial configuration with small individuals in the center has only rarely been described, but it has been found in water insects (male whirligig beetles, Romey 1997; water insects, Sih 1980). It is unclear, however, whether this configuration is consistent in water insects. The converse pattern with large fish in the center is described for a larger number of species of fish, both under ‘undisturbed’ captive conditions (for the hammerhead shark, *Sphyrna lewini*: Klimley 1985; for the bluntnose, *Pimephalus notatus*, and stoneroller minnows, *Campostoma anomalum*: Theodorakis 1989) and under experimental conditions (Krause 1994b; minnows, *Phoxinus phoxinus*: Pitcher, Magurran, and Allan 1986). In relation to SchoolingWorld, it is of interest to know whether and for which species large individuals are missing from the back when large individuals are at the periphery. When large

individuals are in the center, it is of particular interest to note whether clusters of small fish are caught among the large ones for certain compositions of large and small individuals but not for others, as *SchoolingWorld* suggests.

How do these opposite spatial configuration of large and small agents relate to the risk of predation and the competition for food? When, in nature, in schools of certain species, large individuals are continuously in the center, this may be explained by permanent strong cohesion as a consequence of both predator-avoidance and food distribution. If the large ones are in the center only during feeding, this may indicate feeding competition, if food sources are clumped (possibly in hammerhead sharks, Klimley 1985; in minnow, Theodorakis 1989). If this spatial configuration is found only during predator threat (chub, *Leuciscus cephalus*, Krause 1993c), this pattern seems to result primarily from increased cohesion for protection against predators.

The configuration with large ones at the outside would reflect a situation where the group is compact (in loose groups this assortment is lacking) due to predation avoidance and where competition (for whatever it may be) is weak.

Which of the three rules (the ‘active sorting’, the ‘risk avoidance’, or the ‘size difference’ model) protects best against predators, does, of course, depend on the strategy of the predator (whether s/he attacks at the center or at the periphery), but this has not been investigated here.

3.4.4 Conclusion

The two objects of this study are the connection between individual behavior and the collective patterns of (1) density distribution in the schools and school form and of (2) segregation according to familiarity and size. This approach can be extended by adding other features that can lead to spatial segregation, such as age (e.g., in ants, Sendova-Franks and Franks 1995), sex (e.g. Ruckstuhl and Neuhaus 2002), motivation (such as hunger, Krause 1993c), parasites (Krause and Godin 1996), and ecological factors. Possibly, this kind of model may also be made to apply to swarms of other taxa, such as insects. As it is, we hope that our results may inspire empirical scientists to study spatial patterns in schools of real fish and relate their findings to the results of our model.

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Chapter 4

Simulations of the social organization of large schools of fish whose perception is obstructed¹

Abstract

Individual-based models have shown that simple interactions among moving individuals (repulsion, attraction and alignment) result in travelling schools that resemble those of real fish. In most models individuals interact with all neighbours within sensory range which usually includes almost all the individuals of the school. Thus, it implies (almost) global perception. However, in reality in large groups, individuals will only interact with their neighbours close by, because they cannot perceive those farther away, since they are masked by closer ones. Here, we have developed a new model to investigate how such an obstruction of perception influences aspects of social organization in schools of up to 10'000 individuals. We will show that in small schools of up to approximately 30 individuals group shape and density resembles that obtained with global perception, because in small schools hardly anyone is masked by others: school shape is oblong and the density is highest in the frontal half of the school. With increasing group size, from approximately 200 individuals onwards, internal density becomes variable over time, regions of high and low density develop at any location within a school, and group shape becomes more complex, in the sense that inward bounds and appendages occur more frequently. The complexity of shape and internal structure arises because, due to their limited perception, individuals interact relatively more locally in larger schools. In case of global perception, however, shape remains elliptical for all group sizes and in groups above 1000 individuals, the schools become unrealistically dense. In sum, our results show that obstructed perception in itself suffices to generate a realistic organization of large schools and that no extra rules for coping with many individuals are needed.

4.1 Introduction

The flexible coordination of schools of fish, ranging from groups of a few individuals to vast aggregations of millions, has been an enigma for a long time. Recently, computer models based

¹under review

on processes of self-organization (Camazine et al. 2001; Deneubourg and Goss 1989; Hemelrijk 2002b; Hemelrijk and Kunz 2005) have shown that coordination among neighbours suffices to generate collective behaviour that resembles that of schools of fish (Aoki 1982; Couzin et al. 2002; Niwa 1994; Parrish and Viscido 2005; Reuter and Breckling 1994; Reynolds 1987).

Besides, such models may guide empirical studies. For instance, they have predicted that larger schools are denser and more oblong (Hemelrijk 2005; Hemelrijk and Hildenbrandt 2008; Kunz and Hemelrijk 2003). These traits are supposed to be interconnected, schools are more oblong, because the higher density of larger schools forces individuals to avoid others more frequently. Since individuals avoid collisions by slowing down, former neighbours may subsequently move inwards and thus the school becomes more oblong. These predictions were subsequently confirmed in an empirical study (Hemelrijk et al. 2010), in which the 3-dimensional positions of individuals in schools were measured in schools of up to 60 mullets. Empirical results confirmed that larger schools were denser and more oblong (Hemelrijk et al. 2010).

Models of fish schooling have usually been based on three behavioural rules consisting of attraction to others further away, alignment with others at medium distance and avoidance of others that are close by (for a review, see Parrish and Viscido 2005). They differ in a number of traits, such as in whether they are made in two or in three dimensions and in the number of interaction partners to which individuals react. Remarkably, the difference in dimensionality hardly affects results (Hemelrijk 2005; Hemelrijk and Hildenbrandt 2008; Huth and Wissel 1992, 1994a; Kunz and Hemelrijk 2003). However, how many and which neighbours an individual reacts to, matters clearly (Viscido, Parrish, and Grünbaum 2005). Most models employ a metric approach, where individuals interact with all neighbours that are located within a certain radius, i.e. a circular area around the focal individual excluding a blind field at its rear (Couzin et al. 2002; Niwa 1994; Reuter and Breckling 1994; Reynolds 1987). Here, because the range of interaction is constant, the number of interaction partners increases with density of the school. Since larger schools are denser (Hemelrijk 2005; Hemelrijk and Hildenbrandt 2008; Kunz and Hemelrijk 2003; Reuter and Breckling 1994), the number of interaction partners increases with school size. This becomes unrealistic in models of very large groups, in the sense that too many individuals interact (Lemasson, Anderson, and Goodwin 2009; Viscido, Miller, and Wethey 2002) and that group structure collapses (Mogilner et al. 2003). By reducing the range of interaction when local density increases, such a collapse has been avoided in the 3-dimensional model of large groups consisting of up to 2000 individuals by Hemelrijk and Hildenbrandt (2008). In other models, individuals are made to interact with a fixed number of their nearest neighbours, their so-called topological range (Aoki 1982; Hildenbrandt, Carere, and Hemelrijk 2010; Huth and Wissel 1992; Viscido, Parrish, and Grünbaum 2005, 2007), or with the first shell or layer of neighbours around it, as given by a Voronoi tessellation (Gregoire 2003). Such restrictions are, however, unrealistic, because in reality neighbours are sometimes perceived over much larger distances in certain directions than in other directions.

The aim of the present paper is to study the consequences of a more realistic representation of interaction partners: individuals interact with all the neighbours they perceive, i.e. those that are not hidden behind others. We study the effect of such obstructed perception on local density and school shape (its asymmetry, the degree to which it is oblong and the convolutedness of its border) in relation to school size for groups of 10 to 10'000 individuals. Our earlier model (Kunz and Hemelrijk 2003), henceforth referred to as the model with global perception, is taken as a control.

Parameter	Symbol and Value
Body length	$b = 0.2$ m
Cruise speed and s.d. (Gaussian noise)	$v_{\text{crs}} = 0.3$ m/s, $v_{\text{sd}} = 0.03$ m/s
'Default' rate of rotation	$\omega_{\text{def}} = \pi$ rad/s
Interaction radius	$r = 5.0$ m
Blind angle	$\gamma = 60^\circ$
Time step	$\Delta t = 0.2$ s

Table 4.1 – Default parameters of the model. These were kept fixed over all experimental conditions.

4.2 Methods

4.2.1 The model

Our model is an extension of our earlier model described in Kunz and Hemelrijk (2003). It is implemented in the programming language C and consists of a 2-dimensional world that is continuous and infinite. In each simulation step Δt all artificial fish are activated in random order. The individuals behave according to three responses, repulsion away from close by neighbours, alignment with individuals at intermediate distances, and attraction to neighbours at larger distances.

Position, speed and heading. At time t individual i is located at position $\mathbf{x}_i(t)$ and moves with a velocity $\mathbf{v}_i(t)$ during one simulation step Δt . Thus the location is updated as

$$\mathbf{x}_i(t) = \mathbf{x}_i(t - \Delta t) + \mathbf{v}_i(t)\Delta t \quad (4.1)$$

where $\mathbf{x}_i(t - \Delta t)$ is the position of individual i at the previous time step. The velocity $\mathbf{v}_i(t)$ comprises the heading $\alpha_i(t)$ and the speed $v_i(t)$

$$\mathbf{v}_i(t) = \begin{pmatrix} v_i(t) \cos \alpha_i(t) \\ v_i(t) \sin \alpha_i(t) \end{pmatrix} \quad (4.2)$$

of individual i . The speed $v_i(t)$ is set to v_{crs} (Tab. 4.1). It is subjected to Gaussian noise with a standard deviation of v_{sd} . Like in other models, it is independent of the behaviour of other individuals (Aoki 1982; Couzin et al. 2002; Huth and Wissel 1992, 1994a). This seems to be a valid simplification, as similar results are found, irrespective if the individuals adjust their speed to neighbours (Hemelrijk and Hildenbrandt 2008) or not (Kunz and Hemelrijk 2003).

The individual's heading $\alpha_i(t)$ is updated each simulation step as follows

$$\alpha_i(t) = \alpha_i(t - \Delta t) + \omega_i(t)\Delta t \pm \alpha_{\text{sd}} \quad (4.3)$$

where $\alpha_i(t - \Delta t)$ is the individual's heading in the previous time step and $\omega_i(t)$ its rate of turning or rotation, which depends on the interaction with neighbours. The heading $\alpha_i(t)$ is subject to Gaussian noise with a standard deviation of α_{sd} .

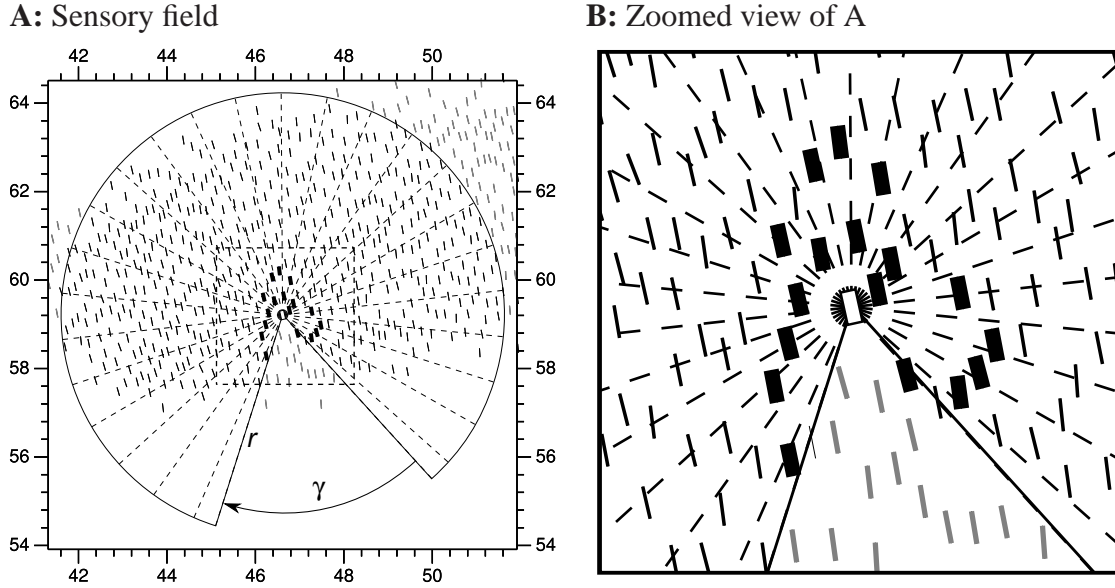


Figure 4.1 – The circular sensory field around an individual (white bar) with the blind angle γ at its back. For obstructed perception the interaction partners are indicated by fat black bars. Interaction partners for global perception are given by the (fat and thin) black bars. Neighbours outside the sensory field are painted gray.

Global and obstructed perception. We use our earlier model as a control (Kunz and Hemelrijk 2003). In this model an individual i interacts with all neighbours located in its sensory field (Fig. 4.1A). In our new model, where perception is obstructed, the interaction partners consist of all those individuals that are not masked by those closer to the focal individual. To find these, we divide the sensory field into sectors and assume that within each sector only the closest neighbour can be perceived (Fig. 4.1AB, fat bars). If this neighbour covers several sectors it is counted only once. Thus, increasing the number of sectors increases the number of different neighbours that may be visible simultaneously.

In relation to each interaction partner j the individual i tends to be repulsed $\omega_{ij}^r(t)$, be attracted $\omega_{ij}^a(t)$ and align $\omega_{ij}^p(t)$. The total behavioural responses of individual i is the sum of the three actions averaged over all its interaction partners. Its rate of rotation is

$$\omega_i(t) = \frac{1}{|P_i(t)|} \sum_{j \in P_i(t)} \omega_{ij}^r(t) + \omega_{ij}^a(t) + \omega_{ij}^p(t) \quad (4.4)$$

where $P_i(t)$ denotes the set of all perceived neighbours (all within the interaction radius for global perception, or those not masked by closer ones for obstructed perception). In other words, individuals do not react to single neighbours independently. Instead, their behaviour is a weighted average of their reaction to all the neighbours perceived by them.

Repulsion, attraction and alignment. The strength of repulsion, attraction and alignment depend in a non-linear and continuous way on the distance d_{ij} between the individuals (inspired by Reuter and Breckling 1994). The weight for repulsion $w_r(d_{ij})$ is highest for short, that for alignment $w_p(d_{ij})$ for intermediate and that for attraction $w_a(d_{ij})$ for longer distances (Fig. 4.2A).

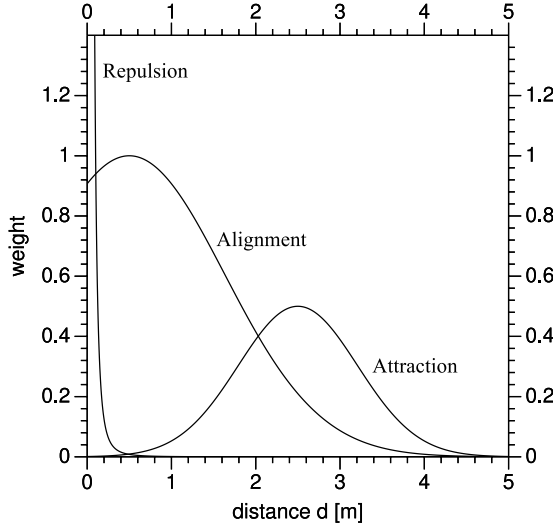
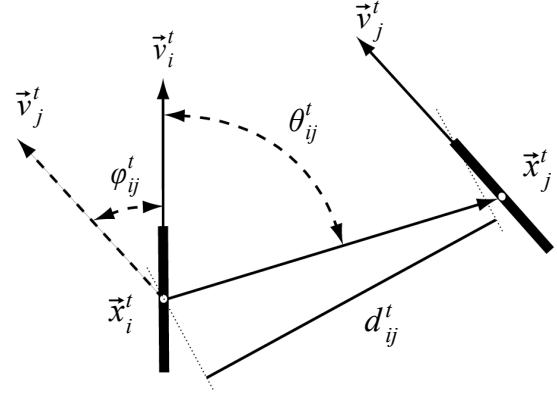
A: Weight factors (obstructed perception)**B:** Angles and vectors between individuals i and j 

Figure 4.2 – A: The weight factors for repulsion $w_r(d)$, attraction $w_a(d)$ and alignment $w_p(d)$ for obstructed perception (the weight factors for global perception are similar, see Kunz and Hemelrijk 2003). d denotes the distance to the neighbour. **B:** The location, headings, associated angles and vectors and bodies of two individuals i and j (black bars).

Repulsion implies that an individual i turns away from a nearby individual j with a rate of rotation (i.e. speed of turning) of

$$\omega_{ij}^r(t) = w_r(d_{ij}) \begin{cases} -\omega_{\text{def}} & \text{if } \theta_{ij}(t) > 0 \\ +\omega_{\text{def}} & \text{otherwise} \end{cases} \quad (4.5)$$

where $w_r(d_{ij})$ is the distance dependent weight factor (Fig. 4.2A), ω_{def} is the 'default' rate of rotation of the individual (Tab. 4.1) and $\theta_{ij}(t)$ is the angle between the vector connecting individuals i and j and the heading of individual i (Fig. 4.2B). Note that the rate of turning $\omega_{ij}^r(t)$ caused by repulsion only depends on the sign of $\theta_{ij}(t)$, such that the individual i turns always away from j .

Attraction implies that individual i turns towards individual j with a rate of rotation of

$$\omega_{ij}^a(t) = w_a(d_{ij})\omega_{\text{def}}\theta_{ij}(t). \quad (4.6)$$

Note that, in contrast to repulsion, the rate of turning $\omega_{ij}^a(t)$ caused by attraction is proportional to $\theta_{ij}(t)$, thus individual i turns faster when the angle to individual j is larger. Therefore, when individual j is directly ahead, i does not turn at all.

Aligning implies that individual i matches its orientation to that of individual j by turning with a rate of rotation of

$$\omega_{ij}^p(t) = w_p(d_{ij})\omega_{\text{def}}\varphi_{ij}(t) \quad (4.7)$$

where $\varphi_{ij}(t)$ is the difference in the headings of the two individuals (Fig. 4.2B). Thus, by turning proportionally to $\varphi_{ij}(t)$, individual i adjusts its heading to that of individual j .

We represent the body of the individual by lines of length b (Tab. 4.1). This influences the degree with which the individual blocks the perception of others (Fig. 4.2A). The distance d_{ij}

Parameters	Global perception	Obstructed perception
Group size	10, 20, 30, 60, 100, 200, 300, 600, 1000	10, 20, 30, 60, 100, 200, 300, 600, 1000, 2000, 3000, 6000, 10'000
Number of perceptual sectors	-	10, 20, 30, 50

Table 4.2 – *Model parameters that differ between experimental conditions.*

between individual j and (the focal) individual i is measured as the distance between individual i 's center and the nearest point of individual j (Fig. 4.2B). Thus, it depends on the orientation of individual j .

4.2.2 Parameterization and initial conditions

Note that for ease of comparison the parameters (Tab. 4.1) are kept identical to those used in our former studies (Hemelrijk and Kunz 2005; Kunz and Hemelrijk 2003). The interaction radius r and the blind angle γ are similar to those used by Reuter and Breckling (1994). Body length l and cruise speed v_{crs} are chosen in a biologically meaningful way (Pitcher and Partridge 1979). The weight factors for repulsion w_r , attraction w_a and alignment w_p are chosen such that for groups between 10 and 100 individuals the nearest neighbour distance corresponds to biological findings (Olst and Hunter 1970; Partridge and Pitcher 1980; Pitcher and Partridge 1979) and are slightly adjusted for obstructed perception, such that groups of 50 individuals with 30 sectors resemble those with global perception. The 'default' turning rate ω_{def} and the variation in speed v_{sd} and heading α_{sd} we have tuned by hand such that individuals are able to avoid others effectively but without introducing too erratic or jerky movements. The initial conditions are chosen such that a single school always forms. Individuals are positioned randomly in a circular area whose radius is chosen such that the initial density is approximately 10 individuals per square meter. They have random orientations chosen from a uniform distribution of angles within a sector of 90 degrees and their velocity is set to the cruise speed v_{crs} .

4.2.3 Experiments and Measures

We study both models for a range of group sizes (Tab. 4.2). For global perception, the largest group size contained 1000 individuals because larger schools were unrealistically dense. We study the influence of the numbers of sectors if perception is obstructed (Tab. 4.2). For each parameter setting 5 replicas are performed. The simulations last for 5000 steps, which corresponds to 1000 s (16.7 min). Unless indicated otherwise, measurements are done every 10 s and are averaged over the time interval between 500 and 1000 s (to avoid transients at the beginning of the simulations). Octave, a high-level language, intended for numerical computations, was used for data analysis.

As a global measure of the average density of individuals in a school we use the average nearest neighbour distance.

We measure shape in two ways: the degree to which a school is longer than wide (oblongness) and asymmetrical. In order to measure the degree with which it is oblong, we enclose the school in the smallest rectangle oriented parallel to its direction of movement (Kunz and Hemelrijk 2003) and measure oblongness as the ratio of the length of the school in its direction

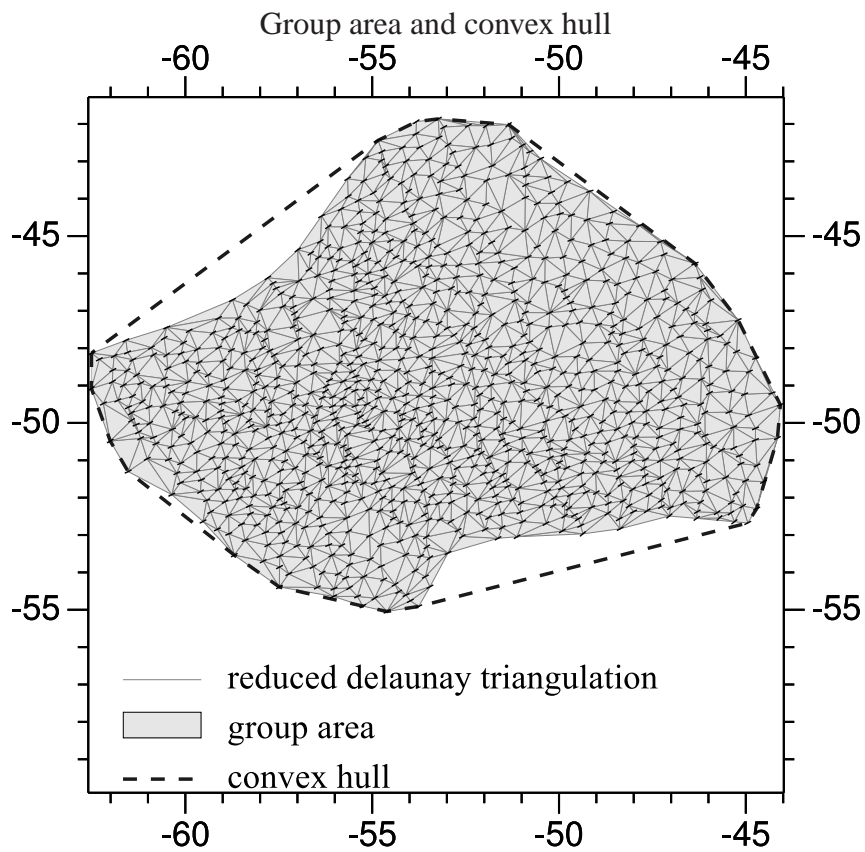


Figure 4.3 – A school of 1000 individuals (black bars). The gray triangles depict the Delaunay triangulation, whereby all triangles with an edge longer than 2 m have been omitted. The dashed perimeter illustrates the convex hull of the school.

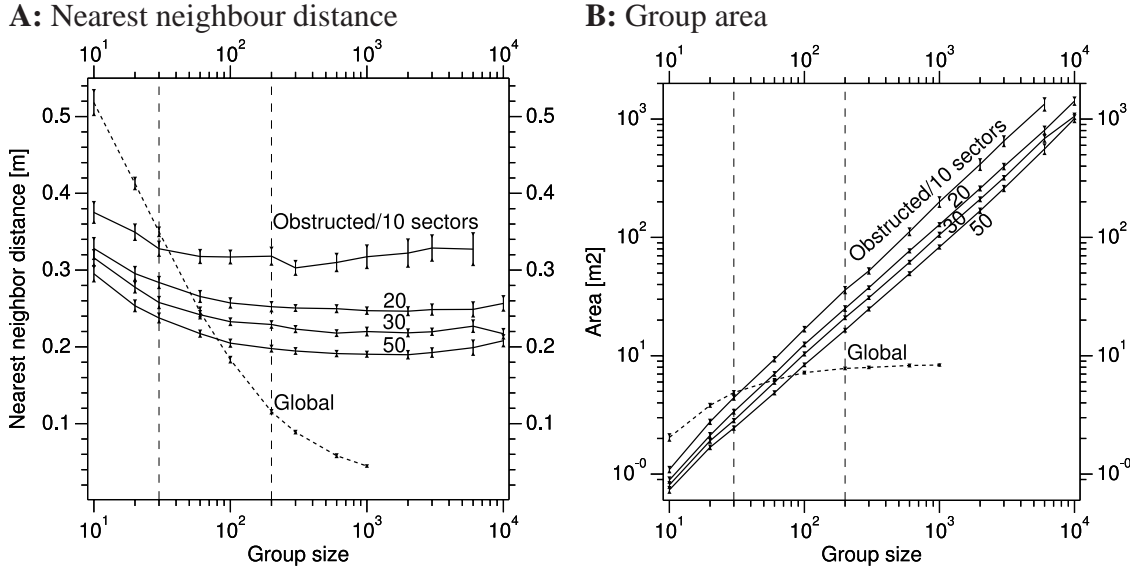


Figure 4.4 – Average nearest neighbour distance (A) and group area (B) for obstructed and global perception. The weight factors (see Methods) are chosen such that nearest neighbour distance is similar for groups of 50 individuals under global and obstructed perception (30 sectors). Therefore, for smaller groups nearest neighbour distance is larger when perception is obstructed. For global perception, schools of more than 1000 individuals become unrealistically dense and when perception is obstructed groups of 10'000 individuals occasionally fragment for 10 sectors; results are thus shown only for smaller groups. Note that A has a half- and B a full-logarithmic scale.

of movement divided by its width. The asymmetry of the school shape (ignoring the movement direction) we compute as the ratio of length and width measured by means of a principle component analysis (PCA) of the positions of the individuals. Length is measured along the largest dimension of the school, which is given by the eigenvector associated with the largest eigenvalue of the co-variance matrix. The width is measured perpendicular to the length. This equals the aspect ratio used by Hildenbrandt, Carere, and Hemelrijk (2010). An asymmetry value of one corresponds to a roughly circular school whereas higher values indicate a more elliptic shape.

We characterize the convolutedness of the group border by calculating its convexity, i.e. the ratio of the group area divided by the area of the convex hull. Group area is measured as the area of the Delaunay triangulation where all triangles with an edge longer than 2 m are omitted (Fig. 4.3) to account for inward bounds. The maximal length of edges (2 m) is chosen as small as possible (for higher accuracy) but large enough to ensure that the Delaunay triangulation does not fragment the school. A convexity close to one indicates a roughly circular or elliptic school, whereas lower values reveal more irregular group shapes with inward bounds and appendages.

4.3 Results

Although it happens to a different degree, for obstructed perception like in the control, i.e. global perception, with increasing group size nearest neighbour distance decreases (Fig. 4.4A),

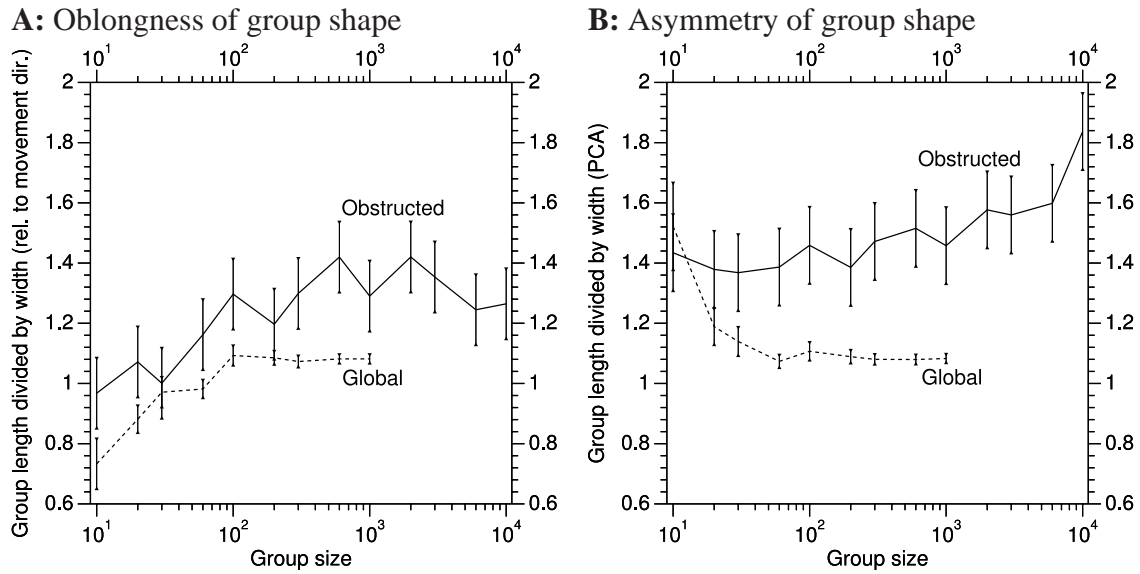


Figure 4.5 – Group shape (measured as length divided by width) relative to the direction of movement, called oblongness (A), and shape measured by the ratio of the longest dimension divided by the one orthogonal to it (independent of the movement direction), called asymmetry (B). As the influence of the number of sectors appears unimportant and because variability is high the plots for obstructed perception are lumped together for all numbers of sectors (10, 20, 30, 50).

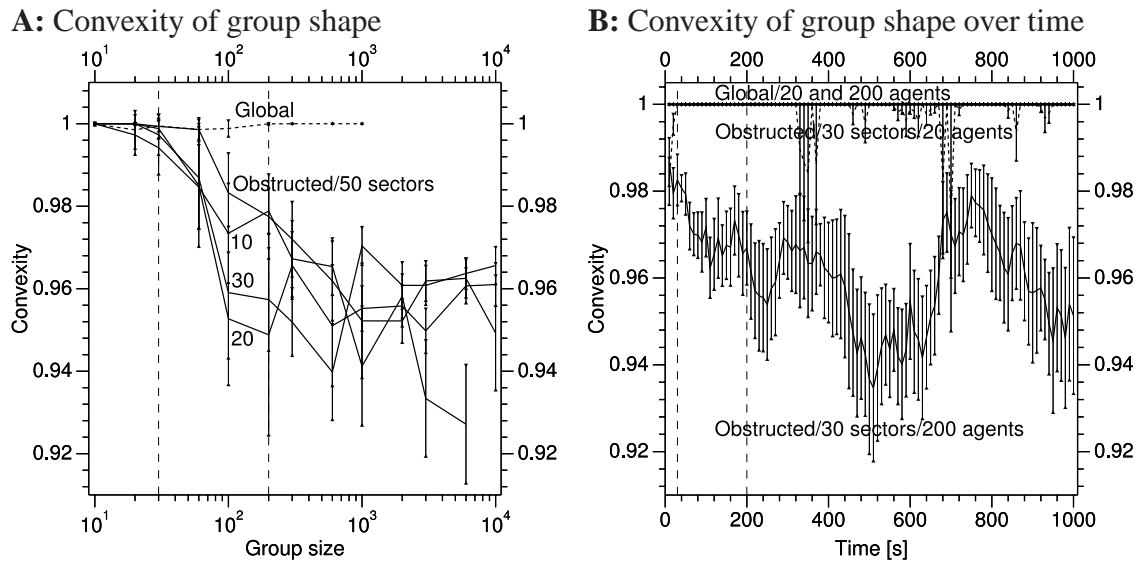


Figure 4.6 – Convexity of group shape (group area divided by the area of the convex hull) vs. group size (A) and over time (B) for groups of 20 and 200 individuals. Note that the plots for global perception and groups of 20 individuals with obstructed perception are almost identical (B).

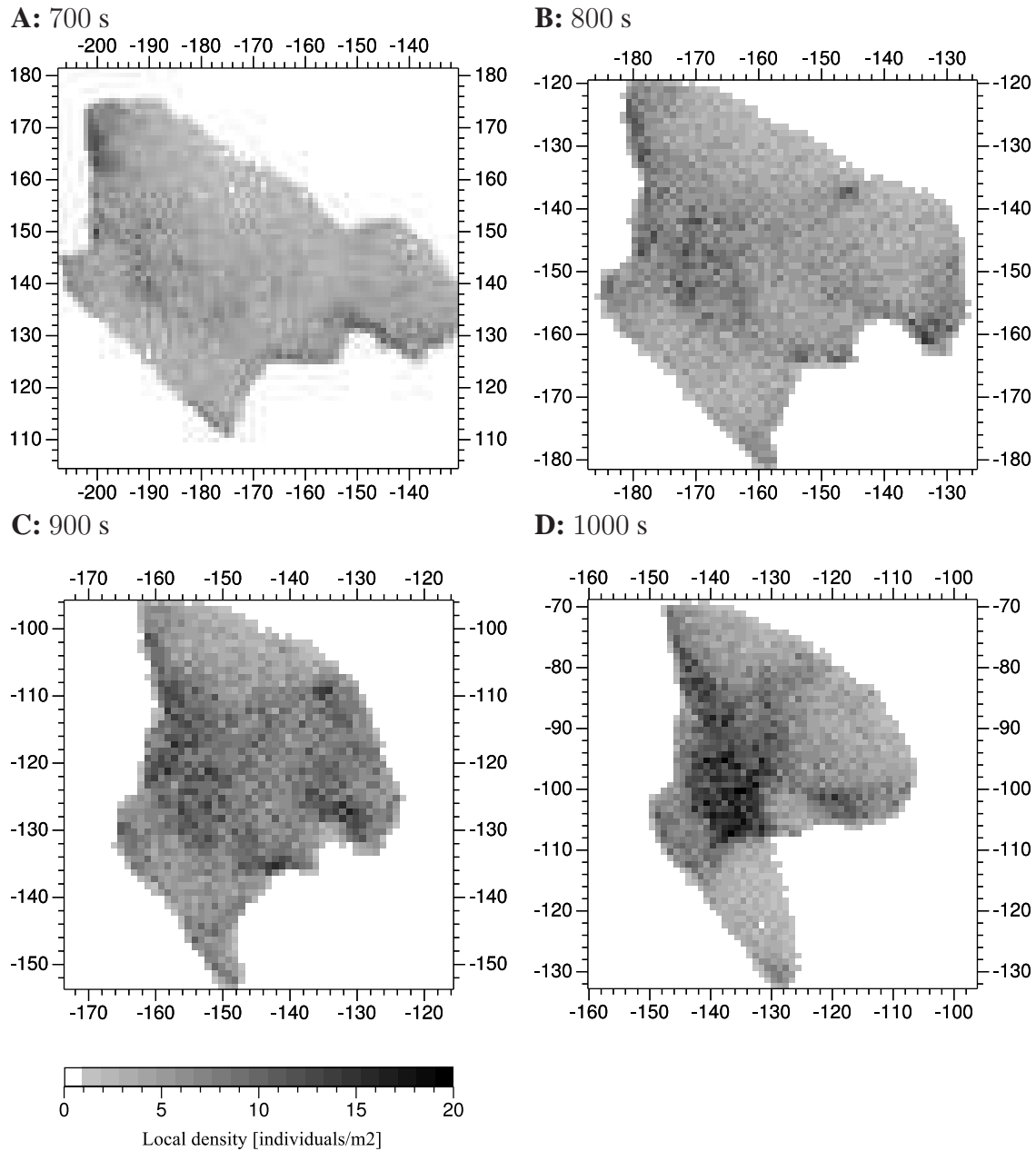


Figure 4.7 – Snapshots of a group of 10'000 individuals at different time steps. Local density is color coded, and ranges from 0 to 20 individuals per square meter.

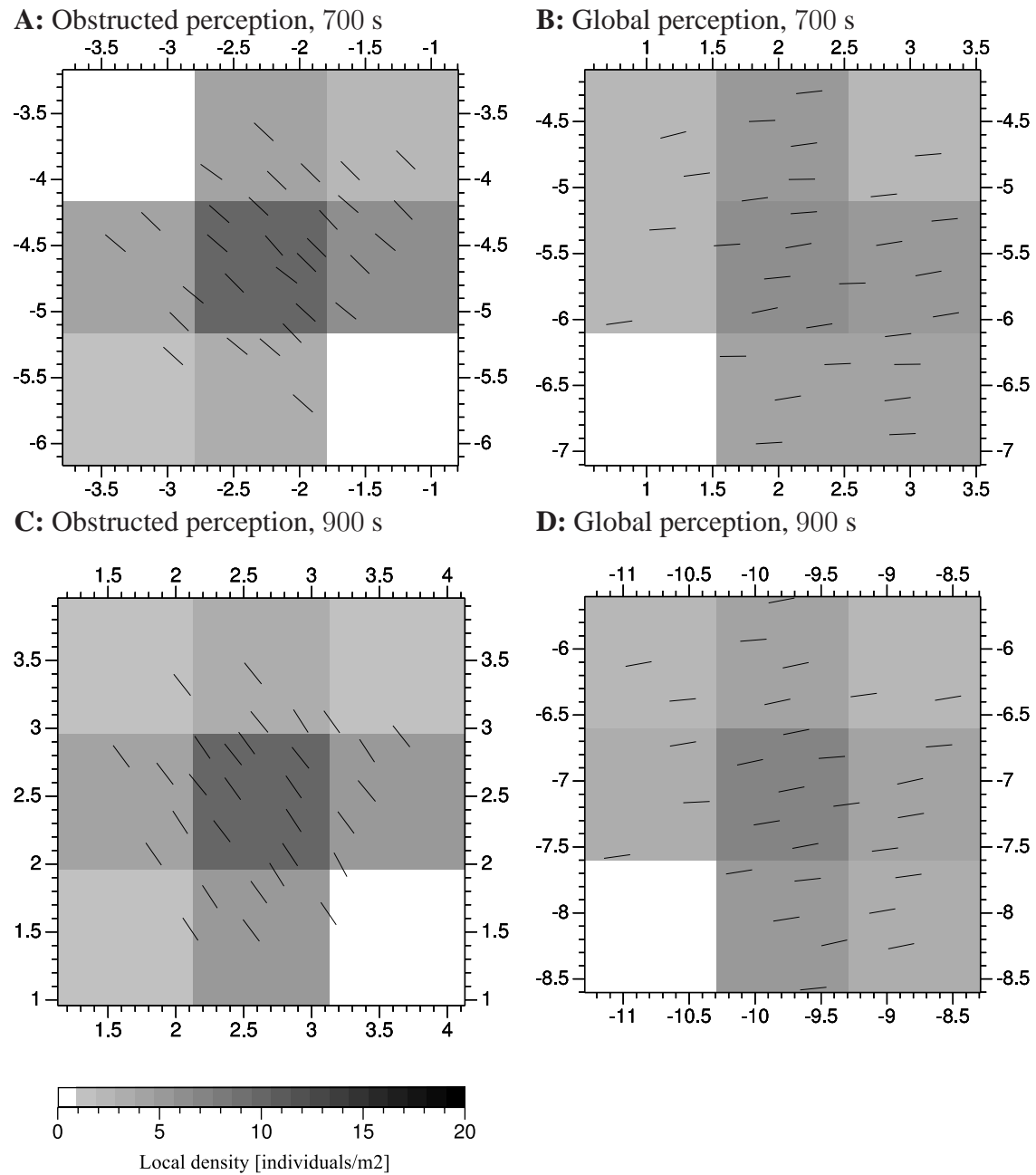


Figure 4.8 – Snapshots of two groups of 30 individuals after 700 and 900 s with obstructed (**AC**) and global perception (**BD**), respectively. Local density is color coded, and ranges from 0 to 10 individuals per square meter. As the weight factors are chosen such that nearest neighbour distance is similar for groups of 50 individuals with obstructed and global perception (Fig. 4.4A), density in groups of 30 individuals under obstructed perception is lower than it is under global perception.

group area increases (Fig. 4.4B) and groups become more oblong (Fig. 4.5A).

However, compared to the control, in which nearest neighbour distance decreases strongly with group size (Fig. 4.4A) and becomes unrealistically small for groups larger than 1000 individuals, when perception is obstructed, nearest neighbour distance decreases with group size less (Fig. 4.4A), leading to more realistic group densities. Because density stabilizes for groups larger than 200 individuals, the surface area of the school increases linearly with school size (Fig. 4.4B). Further, with increasing size, group shape is more oblong and asymmetric (Fig. 4.5AB), more convoluted and thus less convex (Fig. 4.6A) and local density is more heterogeneous (Fig. 4.7): there are regions of higher density at the periphery as well as in the interior and occasionally there are holes. In large groups school shape (Fig. 4.6B) and local density (Fig. 4.7) is more variable over time than it is in small schools (Fig. 4.6B, Fig. 4.8AC) and in case perception is global (Fig. 4.6B, Fig. 4.8BD).

Small groups of up to 30 individuals resemble those in the control model: Nearest neighbour distance decreases with group size (Fig. 4.4A) and group area (Fig. 4.4A) and oblongness increase with group size (Fig. 4.5B); group shape is convex and static over time (Fig. 4.6) and local density is highest in the interior of the school (Fig. 4.8).

Although we did not perform a detailed sensitivity analysis, changing the weight factors for the behavioural responses affects our model in a way similar to that reported by Couzin et al. (2002). Increasing the strength or range of repulsion makes groups sparser, increasing the strength of attraction or its range increases density. Increasing the range of alignment leads to milling, i.e. the groups form a ring. Very strong repulsion or very weak attraction leads to fragmentation of the group, very weak alignment makes the group unordered, so that it becomes stationary.

4.4 Discussion

We developed a new model of schooling, where the interactions among individuals are represented more naturally, because individuals interact only with those neighbours that they can perceive because these neighbours are not masked by closer ones as suggested by Breder Jr. (1954) and Huth and Wissel (1994a).

The differences in nearest neighbour distance, group shape and density between the model with obstructed perception and the control can be explained by the lower number of interaction partners if perception is obstructed. Here, the relative number of interaction partners (i.e. the number of interaction partners divided by group size) decreases with school size, it decreases from 60% in groups of 10 individuals to below 0.2% in groups of 10'000 individuals, but in the control it is always about 80%. Thus interactions are more local. For groups larger than approximately 200 individuals, the number of interaction partners becomes independent of group size because it is at its maximum (between 4 and 11, depending on the number of perceptual sectors) and therefore, nearest neighbour distance stabilizes (Fig. 4.4A). For groups of increasing size the shape of schools is more asymmetric (Fig. 4.5B), more convoluted (Fig. 4.6A) and more variable over time (Fig. 4.6B), because local interaction does not coordinate the group globally, such that subgroups may move in different directions. This causes the formation of 'appendages' and 'inward bounds' and regions of high or low density (Fig. 4.7).

The results are qualitatively similar for different numbers of sectors (Fig. 4.4 and 4.6A). However, nearest neighbour distance and group area are smaller for a higher number of sectors

(Fig. 4.4AB) because of associated higher number of interaction partners and thus the stronger attraction. This higher density at a higher number of influential neighbours confirms the findings in related models by others (Huth and Wissel 1992; Viscido, Parrish, and Grünbaum 2005).

Small groups in our model resemble those in metric models (in which individuals interact with all neighbours within the radius of interaction), but large groups in it resemble those in topological models (in which individuals interact with a fixed number of nearest neighbours). In small groups of up to approximately 30 individuals, the effect of masking is weak and the individuals interact with almost the entire group (the number of interaction partners ranges between 20% and 60% of the whole group). Therefore, results are qualitatively similar to those of metric models: Nearest neighbour distance decreases with increasing group size (Hemelrijk and Hildenbrandt 2008; Kunz and Hemelrijk 2003; Reuter and Breckling 1994), larger groups are increasingly oblong and density is highest in the front half of the school (Hemelrijk and Hildenbrandt 2008; Hemelrijk and Kunz 2005). Note, that the model by Hemelrijk and Hildenbrandt (2008) is only partly metric, because the radius of interaction decreases with increasing local density. Thus, it is keeping the number of interaction partners at around 15 and is thus almost topological for groups larger than 15 individuals.

In groups with more than 200 individuals, most neighbours are hidden behind closer ones, and the number of interaction partners becomes independent of group size like in models with a fixed number of interaction partners (i.e. topological interaction-range). Consequently, the results resemble those of topological models of schools of fish and of flocks of birds: Nearest neighbour distance depends not on group size when group size is significantly larger than the number of interaction partners (Hildenbrandt, Carere, and Hemelrijk 2010; Viscido, Parrish, and Grünbaum 2005). A higher number of interaction partners (i.e. due to a higher number of visual sectors in our model) leads to a shorter nearest neighbour distance (conforming to Huth and Wissel 1992; Viscido, Parrish, and Grünbaum 2005; Warburton and Lazarus 1991).

Apart from these similarities, our model of obstructed perception differs from metric (with fixed interaction ranges) and topological models (with a fixed number of interaction partners) in two important ways: First, the number of interaction partners and the range of interaction varies according to the details of the actors perception of others (depending on local density, body size and number of sectors). Second, in our model individuals perceive others over larger distances in the directions where the density of neighbours is lower and over shorter distances in the direction where density is higher. This is the case for real animals too, particularly if they are located at the border of a group. The necessity to incorporate this in schooling models was already pointed out by Huth and Wissel (1994a). In our model with obstructed perception, individuals at the border of a school are more likely to interact with individuals in a neighbouring school (Fig. 4.9) than if interaction is topological or metric with a short interaction range (Hemelrijk and Hildenbrandt 2008). How such differences in choosing interaction partners influence the formation and maintenance of groups of different sizes, we will investigate in future models.

Results of our model resemble the following empirical data: In small schools of fish of up to 60 individuals of various species (mulletts, minnows, herring, saithe, cod, three-spined sticklebacks and rudd) density increases with group size (Hemelrijk et al. 2010; Keenleyside 1955; Partridge 1980; Partridge et al. 1980). For schools up to 2.2 million individuals (herring, sprat, saithe) the average inter-individual distance varies greatly within and between schools (up to a factor of 100) but does not seem related to school size (Misund 1993); dense areas and regions of almost empty space are found frequently in a few hundred juvenile roach and

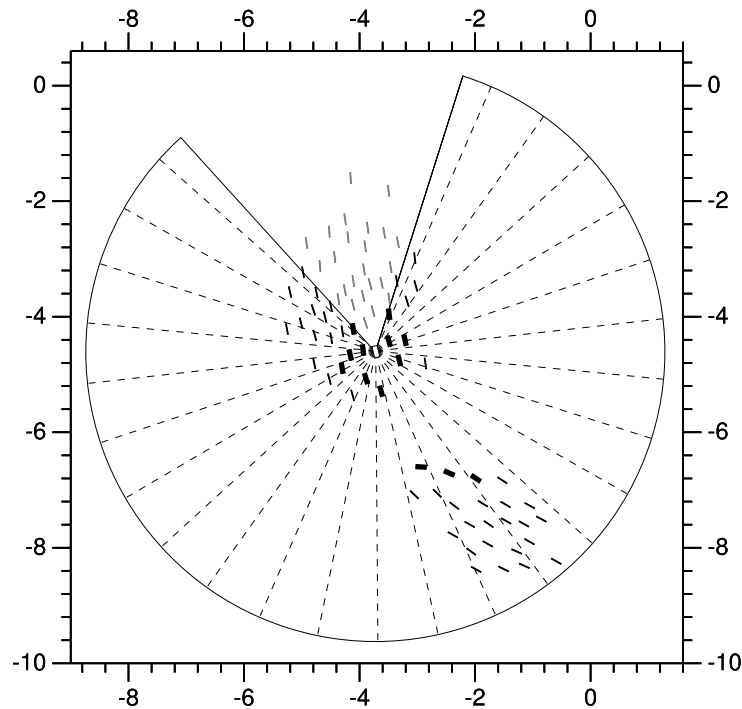


Figure 4.9 – Illustration of the interaction partners (fat black bars) of an individual (white bar) with obstructed perception. As it is close to the border it interacts with distant individuals that are part of another group.

perch (Guillard, Brehmer, and Colon 2006) and in very large schools of many thousands of sardines (Freon, Gerlotto, and Soria 1992; Gerlotto and Paramo 2003). Similarly, in starling flocks ranging between 500 up to 2500 individuals average density varies considerably across flocks (by a factor of 3) but is not associated with the number of birds; regions of high density may occur at any location, also at the border of the group (Ballerini et al. 2008).

Oblong shape is found for small schools of up to 30 herring, saithe and cod (Partridge et al. 1980), 60 mullets (Hemelrijk et al. 2010), a few hundred juvenile roach and perch (Bumann, Krause, and Rubenstein 1997; Guillard, Brehmer, and Colon 2006), a few hundreds of roach and several thousands of minnow (Pitcher 1980) and many thousands of herring (Axelsen et al. 2001) and sardines (Gerlotto and Paramo 2003). Furthermore, group shape becomes increasingly irregular for schools of many thousands of herring (Axelsen et al. 2001), sardines (Gerlotto and Paramo 2003) and anchovy (Squire 1978) and also changes dramatically over time for herring (Pitcher et al. 1996) and anchovy (Squire 1978).

Our model of obstructed perception is, to our knowledge, the first one that can explain the characteristics found in large schools of fish, such as the occurrence of complex and changing school shape and the high variability of the inter-individual distances. Remarkably, despite the disturbances generated by the shape-changes, schools in the model still do not split up.

Note that our model is conceptual. It has not been tuned to match a specific species. Its comparison to empirical data was qualitative only. Furthermore, for the sake of simplicity our model is two-dimensional. Extension of our model to three dimensions would make individuals interact with a greater number of neighbours. Since our results of different numbers of sectors (and thus interacting neighbours) are qualitatively similar, we expect results of a 3-dimensional model to resemble those of a 2-dimensional one.

For future research it is of interest to analyse the resemblance of our model to empirical data quantitatively, especially for large schools of more than 200 individuals because for such large groups the influence of obstruction of perception is strong. For example, it could be studied, whether the dynamics of shape and the spatial distribution of individuals resemble those found in nature (e.g. Misund 1993) or if our model is capable to explain the number and size of vacuoles found in schools of real fish (e.g. Gerlotto and Paramo 2003).

In conclusion, by confining the interaction only to those neighbours that can be perceived, instead of including all neighbours within the interaction radius, the model generates patterns of schooling that are more realistic particularly for large schools. As to the question whether in large groups special coping mechanisms are needed (the topic of this issue), we conclude that in models of self-organized schools, it suffices that perception is obstructed in order to generate patterns that characterize those of very large groups.

Chapter 5

On Prey Grouping and Predator Confusion in Artificial Fish Schools¹

Abstract

In two simulation models the benefit of schooling under predatory pressure is investigated. It appears that if a predator cannot become confused by prey, grouping is seldom beneficial. If prey, however, can confuse a predator, schooling appears to protect prey under a whole range of parameters. Using an evolutionary approach we found that, in the case of a confusable predator, cohesive groups with a consistent forward movement evolve most frequently, but that milling stationary groups also prove to be effective. We suggest that the predator protection in moving and stationary groups rely on different mechanisms, among other things, on a kind of altruistic behavior.

5.1 Introduction

Similar to herds or flocks of other animals many species of fish gather in shoals or schools² without the need for leaders or external cues. Instead, it is thought that the (local) interactions between the group members lead through processes of self-organization (Camazine et al. 2001) to the evident group structure. The character of these local interactions has been the focus of many models, e.g. (Aoki 1982; Huth and Wissel 1992; Niwa 1994). Conceptually these models are identical in that individual fish relate their orientation and speed to that of their neighbors according to a few behavioral rules which we will refer to as avoidance (of collisions), attraction (centering) and alignment (matching speed and orientation). As has been demonstrated by means of computer simulations these behavioral rules lead to schooling behavior which looks natural to the human observer. However, in these models the question of what the benefits are of school formation is not addressed.

Of the many studies of the advantages of schooling (Pitcher and Parrish 1993) there are indications for foraging benefits (Street and Hart 1985), hydrodynamic advantages (Svendsen et al. 2003) and anti-predator functions. Here we will concentrate on the anti-predator function

¹appeared as H. Kunz, T. Züblin, and C. Hemelrijk (2006). „On prey grouping and predator confusion in artificial fish schools“. In: *Artificial Life X*. Cambridge, MA: MIT Press, pp. 365–371

²Groups of fish that aggregate for social reasons are commonly referred to as shoals (Pitcher and Parrish 1993). Schools are shoals that swim coordinated and synchronized.

of schools. We will study prey-survival in a model on direct benefits of schooling (Nishimura 2002; Zheng et al. 2005) and in an evolutionary model (Oboshi et al. 2002).

Shoaling fish counter predator attacks in many ways, e.g. by evasion such as flash expansion or by early detection of attacking predators (Pitcher and Parrish 1993). Whereas these strategies are active and direct reactions of the prey-fish to the presence of a predator or an ongoing attack, we will concentrate on two different effects, namely the effect of grouping itself (it may reduce the probability of being found by the predator) and of confusion of the predator.

Grouping may be advantageous because in water fish shoals are barely better detectable than individuals (Pitcher and Parrish 1993). Therefore, when the visual range is low compared to the speed of the predators and the fish, the predator has a much lower chance of encountering a shoal (because of their low number) than encountering fish that swim independently (as there are many). Nevertheless, Treisman shows that grouping is only beneficial if the predator (once a shoal has been detected) can only eat a small number of individuals while the rest can flee (Treisman 1975). Here, we will nevertheless investigate under which conditions shoals might successfully avoid predators. Confusion of a predator reduces the success of an attack of a predator (Krause and Ruxton 2002; Pitcher and Parrish 1993) due to a multitude of available targets. Correspondingly, the decision of the predator about which individual to attack has been shown to take a longer time for larger shoals (Landeau and Terborgh 1986). The reason for this could be twofold – by overloading the visual system (Broadbent 1965) or by the difficulty of choosing between equal targets, the so-called effect of ‘embarrassment of riches’.

Here we will study the effects of grouping and confusion strategies on prey survival both for schooling and ungrouped prey. In a first model we will show how the number of surviving fish depends on the speed of the predator, the time that is needed to consume a prey fish (handling time) and on whether the predator is confused by too many prey-items or not. Next we will present the behavioral strategies that evolve in prey in an evolutionary model.

It is important to note that in these two models prey cannot perceive the predator, therefore they cannot take any evasive action. This allows us to study the effects of grouping by prey and confusion of the predator independently from other anti-predator behaviors such as evasion and startling. We plan to incorporate evasion strategies in future work.

5.2 Methods

This section outlines the two types of prey agents used in the models and the predator, which is the same for both models.

At the start of each simulation, the prey and the predator were set at random positions with random orientation. The initial positions were confined to a limited area, in order that all the agents were in sensory range.

5.2.1 Predator

The predator agent needs to incorporate the two main effects we are interested in: Handling time and being confused.

Handling time. After the predator caught a fish, it stops for a certain time span, randomly changing its orientation. This reflects the process of consuming a prey.

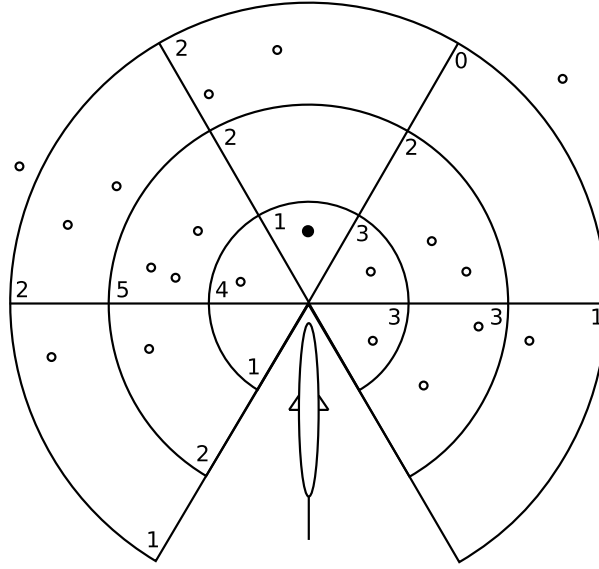


Figure 5.1 – The sensory field of the predator is divided into five sectors that are subdivided in three areas. The crowdedness c_i (identical for all prey in an area) is the sum of the number of fish located in the same area and in the one immediately further away. The higher the crowdedness in an area, the better the protection for the prey due to the confusion effect.

Hunting behavior by confusable predator. To decide which prey to chase the predator assigns an “attractiveness” A_i^c for each prey in its sensory range.

$$A_i^c = \underbrace{\left(1 - \frac{d_i}{d_{\text{view}}}\right)}_{\text{distance factor}} \cdot \underbrace{\frac{0.5}{c_i^2}}_{\substack{\text{confusion factor} \\ (\text{if } c_i > 3)}} \cdot \underbrace{5}_{\substack{\text{prey locking} \\ (i \text{ chased})}} \quad (5.1)$$

Firstly, the attractiveness A_i^c is a linear function of the distance d_i between predator and the prey i ($d_{\text{view}} = 5m$ is the sensory range of the predator). The closer a prey, the higher is its attractiveness. Secondly, to simulate confusion, this “distance factor” is multiplied with a “confusion factor” that reduces the attractivity. c_i (the “crowdedness” of the area where prey i is located) is calculated as indicated in Fig 5.1. For low values of crowdedness ($c_i \leq 3$) the confusion factor is omitted. Thirdly, if the prey i has been chased already in the last time step, it (rather unluckily) gets a bonus in the form of a “prey locking” factor of 5. This is to avoid that the predator keeps switching between prey in situations where several individuals have similar attractiveness. The predator then chases the prey with the highest attractiveness, given that it exceeds a certain threshold.

$$A_i^c > 0.1 \quad (5.2)$$

Once the distance d_i of the chased prey to the predator becomes smaller than $0.1m$ the prey will be killed and eaten. If no prey with attractiveness above threshold is found, the predator moves straight ahead.

parameter	direct effects	evolution	units
no. predators		1	1
handling time	0.2, 1.0, 1.8, 2.6, 3.4	1.0	s
predator speed	0.3, 0.6, 0.9	0.6	$\frac{m}{s}$
number of prey	100	100	
prey behavior	schooling, ungrouped	evolved	
prey speed	0.3	0.3	$\frac{m}{s}$
sensory range ^a	5	5	m
blind angle ^a	60°	60°	
simulation time	100 ^b	1000	s
runs	25 ^c	3 ^c	
size of arena	32 (torus)	32 (torus)	m

^aIdentical for prey and predator

^bNot including the time the predator is eating

^cRandom starting positions, agents in sensory range.

Table 5.1 – Summary of the parameters used.

Hunting behavior by unconfusable predator. The architecture of the unconfusable predator is the same as that of the confusable one, but without the confusion factor.

$$A_i^u = \left(1 - \frac{d_i}{d_{\text{view}}}\right) \cdot \boxed{\text{distance factor}} \cdot \boxed{\text{prey locking}} \quad (5.3)$$

(i chased)

Of prey that are sufficiently attractive $A_i^u > 0.1$ the one with the highest attractivity is chased.

5.2.2 Model on direct effects: schools under predator attack.

Our first model uses a prey agent already developed for previous work. These agents are capable of schooling by the usual behavior, namely turn away from neighbors which are too close, match the swimming direction to the average orientation of neighbors at intermediate distance and turn towards neighbors farther away (see (Kunz and Hemelrijk 2003) for technical details). This model (of one predator and 100 prey agents) was used to investigate the benefits for grouping by prey for a range of parameters (handling time, predator speed) both for confusable and unconfusable predators. The parameters used are summarized in Table 5.1.

5.2.3 Evolutionary model: prey under predatory pressure.

The second model uses an evolutionary approach with a different type of prey agent (see Fig. 5.2). The agent uses a simple neural network to control its movement. The inputs I_j^r are specified in Fig. 5.2. The output O of the network

$$O = f\left(\sum_{j=0}^5 \sum_{r=0}^2 w_j^r \cdot I_j^r\right), \quad f(x) = \frac{1}{1 + e^{-x/1.5}} - 0.5 \quad (5.4)$$

determines the turning angle

$$\phi = 2\pi O, \quad (\phi \text{ clipped to the interval } [-40^\circ, 40^\circ]) \quad (5.5)$$

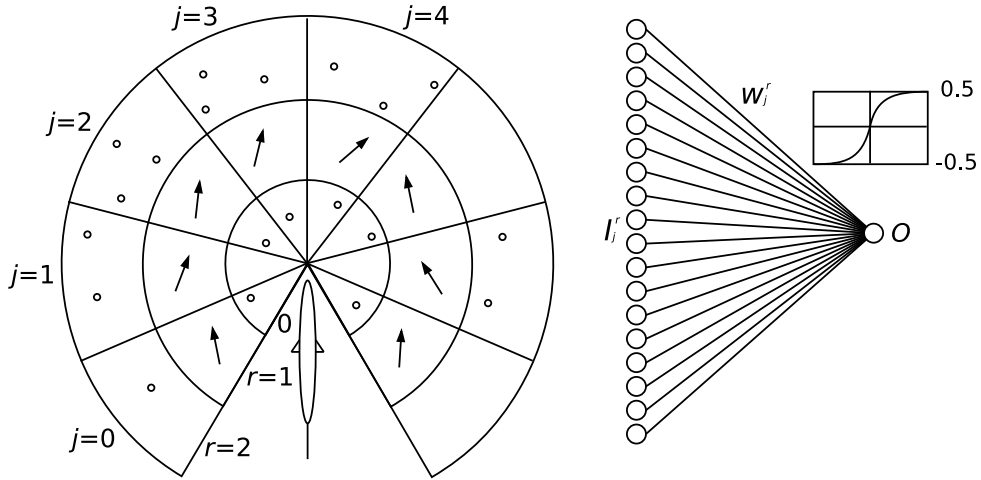


Figure 5.2 – The sensory field of each agent is divided into eight sectors that are subdivided in three areas. A simple neural network is used for the sensory processing. Each input I_j^r node is assigned to an area of the sensory field. Not every area delivers the same information, though. Inputs located in the closest and outermost areas ($r = 0$ and $r = 2$) feed the number of agents (located in that area) into the neural network. Inputs in the intermediate areas ($r = 1$) provide the average relative orientation of the agents located in the respective areas.

and thus the new velocity vector³

$$\angle \mathbf{v}^{t+\Delta t} = \angle \mathbf{v}^t + \phi, \quad \|\mathbf{v}^t\| = 0.3 \frac{m}{s} \quad (5.6)$$

and consequently the movement

$$\mathbf{x}^{t+\Delta t} = \mathbf{x}^t + \mathbf{v}^t \Delta t, \quad \Delta t = 0.2s \quad (5.7)$$

Thus, the weights w_j^r in the neural network determine the prey behavior. Since only unbiased behavior is desired here (i.e. the reaction to neighbors to the left and to the right should be identical) the weights on the right-hand side are determined by the corresponding weights on the left.

The parameters of the predator were chosen deliberately such that grouping would be disadvantageous in the case of an unconfusable predator. For a summary of the used parameters see Table 5.1.

Since we use an evolutionary approach here, we leave it to a genetic algorithm⁴ to find optimal weights for the prey to survive as long as possible. The set of weights therefore constitutes the genome.

The evolutionary algorithm is working on a group of identical prey agents (all have the same genome and thus the same neural network). The groups were evaluated by two criteria, namely the percentage of surviving agents and the ratio of collisions amongst prey agents,

$$\text{fitness} = \frac{n_{\text{alive}}}{n} \left(1 - \frac{n_{\text{collision}}}{n} \right) \quad (5.8)$$

³Prey agents have a constant speed of $0.3m/s$. $\angle \mathbf{v}$ denotes the orientation of the vector \mathbf{v} and $\|\mathbf{v}\|$ its length.

⁴A standard genetic algorithm was used (Goldberg 1989). Our implementation uses `GALIB`, an open source general purpose genetic algorithm library which can be found here: lancet.mit.edu/ga/.

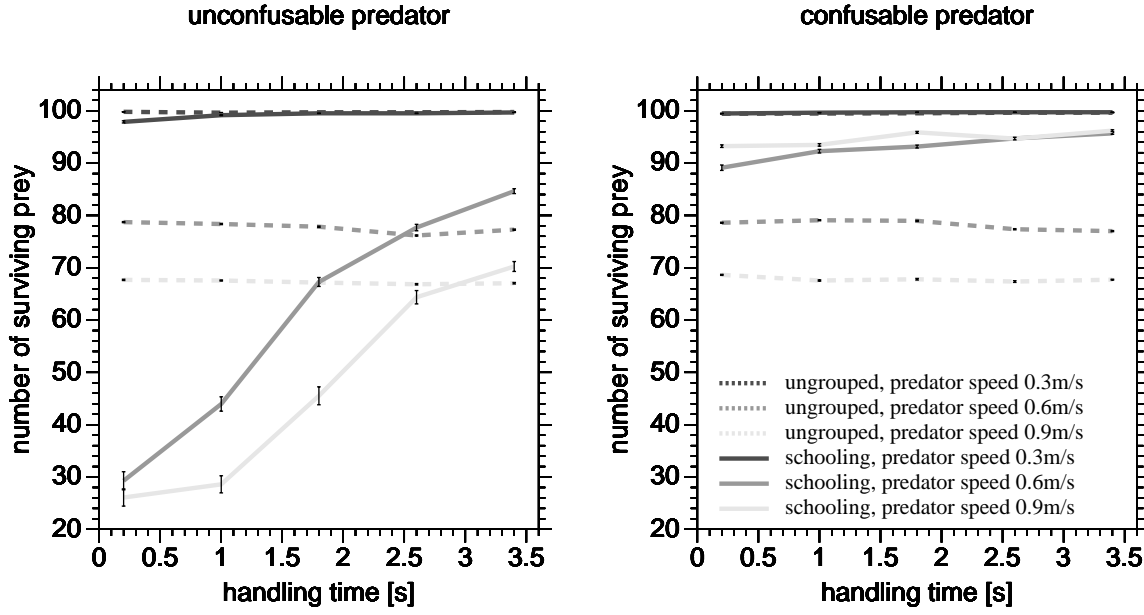


Figure 5.3 – Number of surviving prey. The left panel shows the results of the simulations with an unconfusable predator, the panel on the right depicts the same situation for a confusable predator. Solid lines correspond to schooling prey, whereas dotted lines depict simulations where prey moves independently. The darkness represents the speed of the predator.

where $n = 100$ is the total number of prey agents (at the start of the simulation), n_{alive} is the number of prey agents still alive at the end of the simulation (after 1000 s) and $n_{\text{collision}}$ is the number of prey agents which are closer than 3 cm to their nearest neighbor (measured at the end of the simulation).

A total of 25 evolutionary runs were simulated, in each of which a pool of 30 groups (of 100 individuals and 1 predator) were evolved for 100 generations. In each generation, for each of these 30 groups the fitness (see above) was evaluated.

At the end of a run the group with highest fitness was selected for analysis. Further, each time a prey was captured, its nearest neighbor distance and the average nearest neighbor distance were saved. Additionally, the degree of coordination (see below) was measured at the end of each run.

Statistical measurements

Besides the number of surviving prey the following measures were calculated. To characterize the compactness, we used the average nearest neighbor distance. The degree of alignment is measured by the coordination (polarization) p defined as

$$p = \frac{1}{n} \sum_{i=1}^n \left(1 - \frac{|\angle(\mathbf{v}_i, \mathbf{v}_{\text{avg}})|}{\pi} \right)$$

where \mathbf{v}_i is the velocity of prey i and \mathbf{v}_{avg} is the average velocity over all prey agents. For perfectly coordinated groups we would get $p = 1.0$, for totally uncoordinated groups we would expect $p = 0.5$.

strategy		#	S
schooling	cohesive, consistent forward movement, not necessarily well coordinated	11	80
milling	cohesive, forming a closed loop, stationary	5	82
oscillating	cohesive, agents move synchronously towards and away from the center of the group, stationary	4	78
compact	very dense, stationary or moving	3	69
swarming	cohesive, uncoordinated, stationary	2	62

Table 5.2 – Summary of the evolved grouping strategies. # denotes the number of times the strategy has evolved as the most successful one. 'S' denotes the average number of surviving prey per strategy. Each run started with 100 prey agents.

The degree of 'solitude' indicates the degree with which captured prey were exposed. It is calculated as the ratio of nearest neighbor distance of the captured prey to the average nearest neighbor distance in the group, averaged over all captured prey fish. A solitude of 2 implies that the distance between the captured prey and their nearest neighbor were on average two times larger than the average nearest neighbor distance over all agents. A high solitude thus indicates that the captured prey was isolated and thus not part of a group.

5.3 Results

5.3.1 Direct benefits of schooling

As is shown in Fig. 5.3 (left panel), the number of surviving prey in schools increases when it takes the unconfusable predator more time to handle and eat the prey (solid lines). In contrast, when prey agents are ungrouped, the number of surviving prey does not depend on the handling time. When comparing solid and dotted lines of the same color we can see for which handling time (and predator speed) schooling or independent movement is more advantageous. In fact, for the parameters tested here, the grouping strategy is advantageous only for a very long handling time: for a predator speed of 0.6 m/s handling time should be higher than ≈ 2 s and for a speed of 0.9 m/s handling time should exceed ≈ 3 s.

As expected higher predator speed generally leads to more prey being eaten, both for schooling and non-schooling prey. If the predator has the same speed as the prey, it can hardly capture any of them, despite the fact that the prey does not take any evasive action.

On the other hand, for a confusable predator schooling is always advantageous, even when the predator can consume prey in almost no time (see 5.3, right panel). Note, however, that here we compared only two behavioral strategies, namely schooling and independent movement. There may even be better strategies which we did not test here, whereby individuals group only under certain conditions.

5.3.2 Evolved behavior

The hypothesis here was that a cohesive strategy should evolve among prey agents when under attack of a confusable predator. Remember, that the predator parameters (handling time and speed) were chosen deliberately that the grouping strategy would not work with an unconfusable predator.

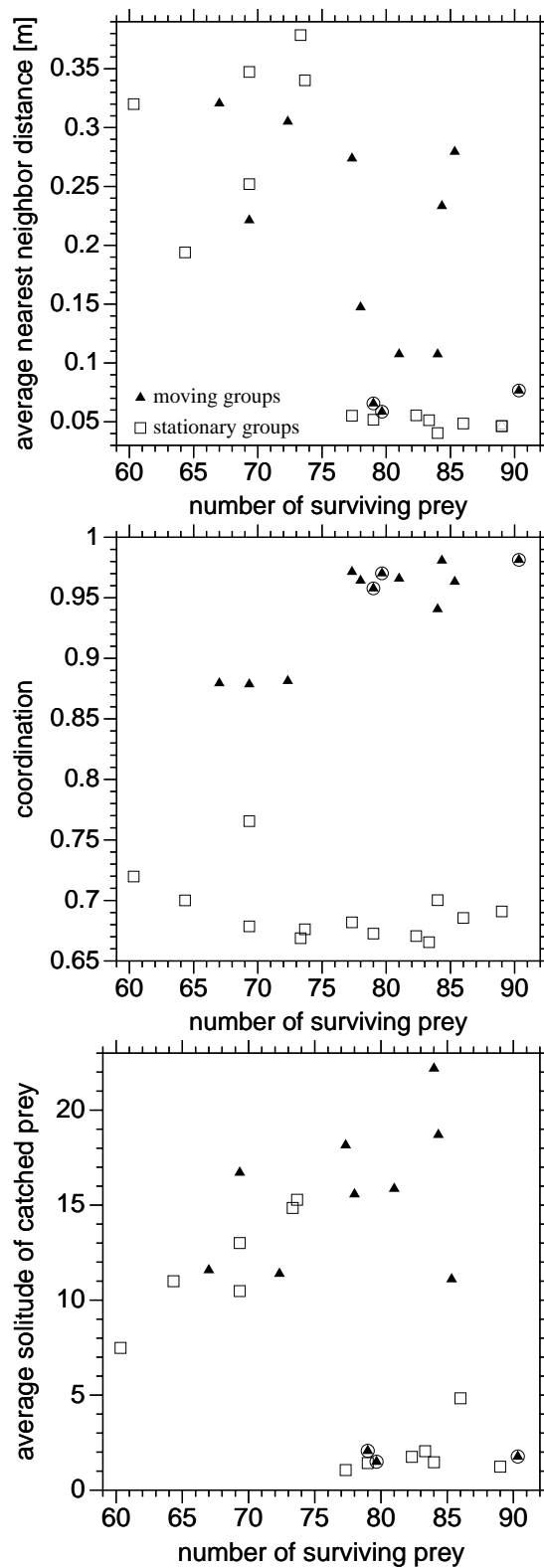


Figure 5.4 – *Nearest neighbor distance, coordination and solitude over the number of surviving prey. The squares correspond to stationary groups, the triangles to moving ones. The circled triangles denote moving groups with a different strategy. For details see the text.*

Indeed, in all the 25 evolutionary runs cohesive strategies proved to be the most successful ones. In none of these strategies were the prey agents moving independently. Nevertheless, the strategies were not identical, see Table 5.2 for a summary⁵. Notably, in almost half of the runs schooling evolved. Interestingly, the second most frequent strategy was milling⁶, a behavior which can also be observed in nature. The next frequent behavior, which we called ‘oscillating’ (where the individuals synchronously approach the group center and then again move away from it repeatedly), is not observed in nature, still it leads to similar good results as schooling and milling. Both the compact and the swarming strategies had a slightly lower number of surviving prey. Although, one would expect that compact groups would yield a better protection than less dense ones due to the confusion effect. The reason that the compact groups had a lower number of surviving prey can be explained by the observation that frequently individuals left the group, in one case the group dissolved entirely. Solitary prey is easily captured by the predator. The swarming groups had the lowest number of surviving prey, because of their low density at the periphery which reduced their protection by the group.

Nearest neighbor distance and coordination. We can get a more quantitative view of the evolved grouping strategies looking at average nearest neighbor distance and the degree of coordination. For both moving and stationary groups there seems to be a tendency that denser groups (with a lower average nearest neighbor distance) offer greater safety in terms of the confusion effect (see Fig. 5.4, left panel). Further, it seems that for stationary groups (red squares) the sheltering effect of dense groups is more important.

The importance of degree of coordination for survival is not immediate (see 5.4, middle panel). Obviously, the moving groups have a much higher coordination than the stationary ones (consistent forward movement requires a certain degree of coordination). Further, it seems that for stationary groups, coordination is of less importance. For the moving groups, on the other hand, a higher coordination indeed seems to correspond to a higher number of surviving prey. This could indicate, that for moving groups, the velocity⁷ of the group is important.

Solitary agents. From the visual inspection of the simulations we knew that in many cases single agents left the group and were often chased (and eaten) by the predator. While bad for the individual, this behavior is potentially good for the group, as it distracts the predator from the group.

While this idea seems straightforward Fig. 5.4 (right panel) shows a more complicated picture. For the stationary groups it seems that such ‘altruistic’ behavior does not really help the group, as indicated by a low solitude for the groups with a number of surviving prey > 75 and lower numbers of surviving prey for the groups with a higher solitude. An explanation for this finding may be that solitary agents are captured quickly while the group is still in the sensory range of the predator (and can easily be attacked again). As the stationary groups cannot evade the predator (when the latter is handling a prey item) they have to rely on the confusion of the predator, which is reflected in small nearest neighbor distances (at least for the more successful groups, see also above).

⁵The different strategies were discriminated by a human observer.

⁶Although the average number of surviving prey was slightly higher for milling than for schooling, we do not consider this difference as statistically significant because of the low number of samples.

⁷As the velocity is strongly connected to coordination (Kunz and Hemelrijk 2003).

In moving groups (especially in the more successful ones with number of surviving prey > 75) prey is often captured at a much larger distance from the group than for stationary groups. This means that in these cases solitary prey is captured by the predator, indicating that this ‘altruistic’ behavior of some prey agents is beneficial for the group. Indeed, as the group is moving it may evade the predator when the latter is chasing a solitary prey.

Note, however, that there are also highly successful moving groups where the solitude of captured prey is low (see circled triangles in Fig. 5.4). These groups are protected by confusing the predator because of their small nearest neighbor distance.

5.4 Discussion

In this study, the benefit of schooling (or cohesive behavior in general) under predatory pressure was investigated. Even though the prey agents could not perceive the predator (and thus they could not take any evasive action) it was still beneficial under a wide range of parameters to form groups.

In the model of direct effects of predation on schooling it appears that if a predator cannot become confused by prey, grouping is seldom beneficial. It is only advantageous if the handling time by the predator of the prey is long, so that the predator loses contact with the school while still eating its captured prey. Although predator speed has a strong effect on how many prey agents can escape from the predator, it does not greatly influence what the minimal handling time is under which schooling is beneficial.

If, however, a predator can be confused, schooling appears to be advantageous under a whole range of parameters, even if the predator handles each prey item very fast. This confirms that “the confusion effect is one of the most powerful forces that promote sociality in animals” (Landeau and Terborgh 1986).

Next, an evolutionary approach was used to search for an optimal strategy. We found that in the case of a confusable predator cohesive groups with a consistent forward movement, i.e. schools, evolved most frequently. Although these groups had a considerable degree of coordination (otherwise they would be incapable of maintaining a forward movement) they lacked the high degree of coordination observed in real fish schools. Because it is possible to evolve highly coordinated behavior using our prey model⁸, the only explanation for the low degrees of coordination evolved here is that it is advantageous, because it causes single individuals to stray away from the group and these ‘altruists’ are more likely to be eaten and in this way help the group. We may hypothesize that strongly coordinated schools may evolve under slightly different circumstances, namely when a kind of energy minimization is involved (synchronized movement is considered to be more energy efficient) or when the prey agent can sense the predator and take evasive action (as synchronization is a strong mechanism to transfer information from one part of the group, were a predator has already been detected, to a different part, were the predator cannot be seen).

The second most frequent strategy that emerged was milling – a behavior which is also observed in real fish schools. This unexpected finding is interesting because milling, rather than being a “trap” for fish schools, appears to be beneficial as an anti-predatory strategy – at

⁸Evidence for highly coordinated behavior was found in a separate set of evolutionary runs using the same prey model, but where the prey was explicitly selected for a high degree of coordination (data not published here).

least in our experiments. Whether milling in real fish schools also serves as a protection against predators is, to our knowledge, an open question.

The third most frequent strategy that evolved we called ‘oscillating’. This has not been observed in real fish schools, possibly because this behavior would be energy expensive.

Another strategy that emerged, which we called ‘compact’, has also been observed in real fish schools. Under predatory attack prey may form very densely packed groups, which makes it very difficult for the predator to single out individuals to attack (Hamilton 1971).

The last strategy that evolved, namely swarming (or shoaling) is observed also in nature. Nevertheless, this strategy did not seem to be particularly effective in protecting the group against the predator.

When comparing stationary groups with moving ones in terms of average nearest neighbor distance and solitude, it seems that the predator protection may depend on two different mechanisms. Most of the more successful stationary groups are very dense ($nnd \approx 5$ cm) and almost no prey agents leave the group. In contrast, for many (but not all) moving groups the nearest neighbor distance is much higher and a high fraction of the killed prey was captured outside of the group. For the few moving groups without solitary individuals nearest neighbor distances appears to be low. This suggests that the stationary groups and the moving groups without solitary individuals rely entirely on the protective effect of confusing the predator, whereas other moving groups employ a combined strategy, of on the one hand confusion and on the other hand avoidance by swimming away from the predator if it is busy chasing a prey that left the group.

Chapter 6

Summary and Discussion

This chapter concludes this thesis by summarizing the results obtained and discussing more general principles that can be drawn from them. We finish up with suggestions for future research.

6.1 Summary

Here we will summarize the results from the previous chapters, focused, however, on those that are consequences of the individuals' embodiment and situatedness. For more details, the reader is referred to the respective chapters.

Of course, all the results presented here primarily emerge from the interactions among the individuals and are therefore a consequence of self-organization. Thus, the results we discuss here are those that arise as embodiment and situatedness shape the interaction among the individuals, thereby affecting the process of self-organization and thus the patterns that emerge.

6.1.1 Effects of embodiment

In chapter 2 the implications of body size and form on the social organization of fish schools consisting either of large or small individuals is investigated.

Body size directly affects the *inter-individual spacing*: Larger individuals occupy more space (because their body is larger) and avoid neighbors at larger distances, therefore schools of large individuals are less dense and occupy a larger area than those of small individuals.

The asymmetric body form leads to *less uniform inter-individual spacing*: Because of the elongated shape of the body individuals maintain larger distances to neighbors ahead than to those at the sides (measured as distance from center of mass of one individual to that of the other).

Body size influences the *polarization* and *speed* of the schools: Because large individuals align with neighbors further away, schools of large individuals are more polarized than those of small ones. They are also faster as a group (note that in our model large and small individuals have the same preferred speed), because in highly coordinated schools all individuals swim in the same direction.

However, if body form is also reflected in the shape of the regions of repulsion and alignment (elliptic agents), the situation reverses, because of the *repeated repulsion effect*, which is

stronger for large individuals. Consequently, groups of large individuals are less polarized and thus slower than those of small ones.

In chapter 3 the effect of body size and form on the organization of mixed schools of large and small individuals is investigated.

Body size has a strong effect on the *positioning* of the individuals within the school: Because large individuals maintain larger inter-individual distances they avoid small individuals stronger than vice versa. Consequently, over time, they are pushed to the periphery, while the small ones remain in the center.

However, if small individuals avoid to be in the vicinity of large individuals (risk avoidance) but still maintain smaller distances among themselves, then the pattern reverses, with small ones at the periphery and large ones in the center.

6.1.2 Effects of situatedness

In chapter 4 individuals are made more situated by including the masking of distant neighbors by closer ones. Such an obstructed perception has a big impact on the density and the form of large groups.

Without obstruction increasing group size leads to increasingly dense groups, because in larger groups more individuals interact, which leads to stronger mutual attraction. In fact, because of the high density the interaction becomes almost global (because most of the neighbors are within interaction range) and thus the groups have a very regular, approximately elliptic form.

With obstructed perception, on the other hand, the number of influential neighbors decreases with increasing density, because crowding limits the perception of others. In fact, the masking of distant neighbors by closer ones restricts the interaction to the *local environment* of an individual. Whereas for small groups, obstructed perception has little effect, because here only a few neighbors are hidden behind others, for groups larger than 200 individuals there are several profound consequences, which are due to the more local interaction.

First, the average nearest neighbor distance (or group density) becomes *independent of group size*, thereby avoiding unrealistically dense groups that occur with the old model.

Second, group shape becomes more *convoluted or amoeboid*, with appendages and inward bounds. Furthermore, group shape *changes over time*, sometimes dramatically.

Third, local density becomes *more heterogeneous*, with regions of higher and lower densities, respectively, occurring in the interior as well as at the boundaries. Additionally, the distribution of individual densities undergoes *heavy fluctuations*, when the overall shape of the group changes.

In chapter 5 a series of experiments was performed with a predator that was confusable, thereby approximating the perceptual limits of a real predator and thus making the simulated predator better situated.

Using such a predator as “implicit fitness function” (by counting the number of surviving prey after a given amount of time) it was straightforward to *evolve schooling behavior* (and other related grouping strategies, such as milling) using genetic algorithms.

Furthermore, if a predator is confusable, schooling is advantageous under a wide range of predator parameters (predator speed and food handling time), whereas if the predator is not confused by prey, grouping is only beneficial if food handling time is very large.

6.2 Conclusions

Whereas in biology, the morphology of the animals, as well as their sensory and motor system, and how they are situated in the real world has always been part of the research because their significance for explaining natural behavior is obvious. However, the influence of embodiment and situatedness on group behavior has been modeled only in a limited sense so far. As such models are developed to investigate the behavior of animal groups, rather than single individuals, their focus is on the interaction between the individuals, and they abstract from the details of embodiment and how it influences their behavior, i.e. their movement.

On one hand, this abstraction is important, because it let's us build simple models in order to understand the mechanisms how groups organize themselves, or, in other words, how the behavior at the group-level emerges (by self-organization) from the interactions at the individual-level.

On the other hand, once a basic understanding of these processes has been gained, we are ready to explore how they are affected if aspects of embodiment and situatedness are included, which we did here.

6.2.1 Implications of embodiment

In chapter 3 we show that the inclusion of characteristics of the embodiment of individuals leads to sorting of schools according to their body size. This is notable for three reasons. First, the sorting is emergent, as the individuals have no preferences for neighbors of either size, they treat all neighbors equally. Second, also the movement of the small one towards the center and of the large ones towards the periphery is emergent, because none of the individuals have any preferences on their positioning withing the school. And last but not least, it is in a way surprising that size sorting occurs at all, because the individuals do not even know how large their neighbors are.

Thus, rather than being specified explicitly, segregation of individuals according to their body size in our model is entirely passive.

In embodied artificial intelligence, the idea that not every pattern or behavior has to be the result of an explicit mechanism is known as *principle of cheap design* (Pfeifer and Scheier 1999). It states that good designs exploit the physics of the system-environment interaction, or in our case the physically-inspired interaction between the individuals, because they, as we have seen, may lead to emergent phenomena, such as size sorting. In this sense, such models are “cheap” or parsimonious.

6.2.2 Implications of situatedness

The credo of embodied artificial intelligence, that agents need to be situated can be applied to individual-based simulations: In order to develop meaningful models, we have to adopt the individual's perspective. Otherwise, our models may be based on unrealistic assumptions and are, from a biological perspective, meaningless or lead to misleading conclusions.

For example, models based on a metric selection criterion to determine the influential neighbors have a fundamental problem. First, the interaction range has to be big, in order that the individuals can find each other and form a group in the first place. Once the group is formed,

many individuals are within range, which leads to interactions among very many, if not all, individuals.

While this is not a problem for smaller groups, such a high degree of interaction is clearly implausible for larger groups, because the interaction with hundreds of neighbors will overload even the fastest sensory and cognitive system. Besides that, as we demonstrated, it leads to unrealistically dense groups.

The latter has already been realized earlier by Mogilner et al. (2003), who gave exact mathematical requirements for repulsion- and attraction functions to achieve reasonable inter-individual spacing in groups of arbitrary size.

Here, however, we realized that the flaw of our model is not that the repulsion behavior is too weak to compensate for the increasing mutual attraction in groups of increasing size, but that the assumption that individuals interact with all their neighbors within a given range is wrong.

Instead of tweaking the behavioral responses, in chapter 4 we made our individuals more situated, by restricting the interaction partners to those that can be perceived, i.e. those are not hidden behind closer ones. This reduces the number of interaction partners and therefore avoids unrealistically high densities in large groups.

Again, by exploiting “physical” properties of the interaction among the individuals, i.e. by applying the principle of cheap design, we arrive at a model, which has more explanatory power, because it incorporates a real mechanism instead of tweaking model parameters until the results matches biological data or our expectations.

Interestingly, obstructed perception adds adaptivity to the model. If density is high, an individual interacts only with very few neighbors, thereby reducing mutual attraction. On the other hand, if density is low, many more neighbors can be perceived, thereby increasing the overall attraction. In both cases, by regulating the number of interaction partners, obstructed perception stabilizes the school’s density, such that it becomes independent of group size.

6.2.3 Interactions between embodiment and situatedness

A novel characteristic of our model of obstructed perception (chapter 4) is that perceivability and therefore interaction depend also on body size, form and orientation of the close by neighbors, i.e. on their embodiment. First, for large individuals masking is stronger than for small ones (because their larger bodies occlude a larger angle) leading to a lower number of influential neighbors in groups of large individuals.

Second, because of their elongated body, neighbors at the sides occlude a larger angle than those at the front (assuming that individuals are aligned). Therefore individuals interact with more neighbors ahead that are also farther away on average. This leads to an emergent front priority, which has been built into earlier models explicitly (Huth and Wissel 1992, 1994a; Inada and Kawachi 2002; Lukeman, Li, and Edelstein-Keshet 2010) and has also been suggested for real fish (Olst and Hunter 1970; Partridge and Pitcher 1980; Partridge et al. 1980).

Here, situatedness and embodiment of the individuals play together, and provide “for free” (cheap design) what otherwise has to be built into models explicitly, thereby increasing the explanatory power of the model.

6.2.4 Implications on computational efficiency

A major difficulty in the simulation of large schools is the computational effort required to determine the interactions among the individuals, because the number of possible interactions grows very quickly when the number of individuals is increased (see also Appendix A).

As we have seen, making individuals more situated, leads to much less interaction among individuals. Thus, such a model has the potential to be computationally much more efficient than one where the interactions are extensive – if we can devise a method that provides us with the interaction partners without having to examine all pairs of individuals. Indeed, inspired by methods developed originally for astrophysical simulations, we could devise a method to determine the perceivable neighbors without much overhead (see Appendix A for more details).

Thus, the restrictions imposed on the interaction by enhancing the situatedness of the individuals makes the simulation computationally much more efficient, which in turn allows us to simulate much larger groups than otherwise would be possible.

6.2.5 Outlook

In this thesis, we demonstrated that modeling the individuals' embodiment and situatedness more accurately lead to more realistic social organization of simulated fish schools. It is therefore important to include such characteristics in computer-based simulation models and we hope that our results may provide inspiration for further modeling also of other biological systems.

We believe that the principle of cheap design deserves special attention. In its original meaning this principle urges the designer to exploit what is already there in the physical world, instead of devising a specific mechanism. Unfortunately, in simulation models nothing is “already there”. But, at least when modeling biological systems, it is still important to include in the model, what would be “already there” in the physical world, even though this requires a modeling effort. Otherwise our models are in danger of missing important mechanisms, which are present in the real world. Mechanisms that lead to phenomena like the emergent size sorting in the case of reflecting body size in the model, or to the self-stabilization of school density in case of obstructed perception. Without these physically inspired mechanisms we would have to build those things into our models by other means.

Thus, by the inclusion of physical properties, i.e. by modeling embodiment and situatedness more realistically, our explanations of the individuals' behavior get simpler or more parsimonious.

Of course our implementations of embodiment and situatedness are only a first step. For example, we entirely neglected hydrodynamics or the bending of the individuals body during swimming. Furthermore, our implementation of obstructed perception is only an approximation, as fish can be partly occluded, for example, which does not occur in our model. Furthermore, we assumed that the individuals can assess the direction and distance to neighbors as well as their heading and speed, without asking how fish might acquire this information.

Truly embodied and situated models will have to address these challenges. However, we believe that much can be learned on how real fish school by refining our models in this way.

More generally, since in most individual-based models, not only those of schooling, morphological and material constraints are taken into account only in a very limited sense, we expect that their inclusion might in fact lead to surprising insights and to models with higher explanatory power, also for other types of group behavior.

Appendix A

Computational efficiency

A major difficulty in the simulation of large schools is the computational effort required to find, for every individual, the neighbors to interact with. The direct approach, that is used most commonly, is to check for every $N(N - 1) \approx N^2$ pair of individuals if the individuals are in sensory range and thus interact. The computational complexity of this naïve approach is $O(N^2)$ and therefore only suitable for small populations.

To simulate large schools we developed a new method to find nearby neighbors efficiently, which is inspired by an algorithm developed originally for astro-physical simulations (see e.g. Barnes and Hut 1986). Here, at every time step the individuals are sorted into a spatial-tree which is then used by every individual to find the perceivable neighbors. The spatial tree, which provides a hierarchical subdivision of the space into cells (see Fig. A.2A), is constructed as follows:

1. A single square cell that contains all individuals serves as the root of the tree.
2. Every cell containing more than one individual is subdivided into four equally sized cells, which are inserted into the tree as descendants of the parent cell.
3. Step 2 is repeated until each cell is either empty or contains at most one individual.

After constructing the tree each individual uses it to find the nearest neighbor per sensory sector (see Fig. A.2B), i.e. the perceivable neighbors:

1. Starting from the cell containing all individuals, the sub-cells are considered recursively.
2. The sub-cells close to the individual are examined first, and then those further away.
3. If a sub-cell is not in sensory range or is occluded by closer neighbors, then there is no need to process it (and its sub-cells) any further. Note that such a cell might contain many sub-cells and thus a large number of individuals which can all be ignored.

Such a tree-based scheme reduces the computational complexity to $O(N \log N)$ (see e.g. Barnes and Hut 1986). To compare the computational efficiency of the two algorithms or models, respectively, we compare the average number of evaluations of neighbors that are required to find the interaction partners per individual per time-step. For the naïve algorithm used with global perceptions this is always $N - 1$. For the tree-method used together with perceptual obstruction it depends on the number of sensory sectors (see Fig. A.2) but the number of evaluations it is

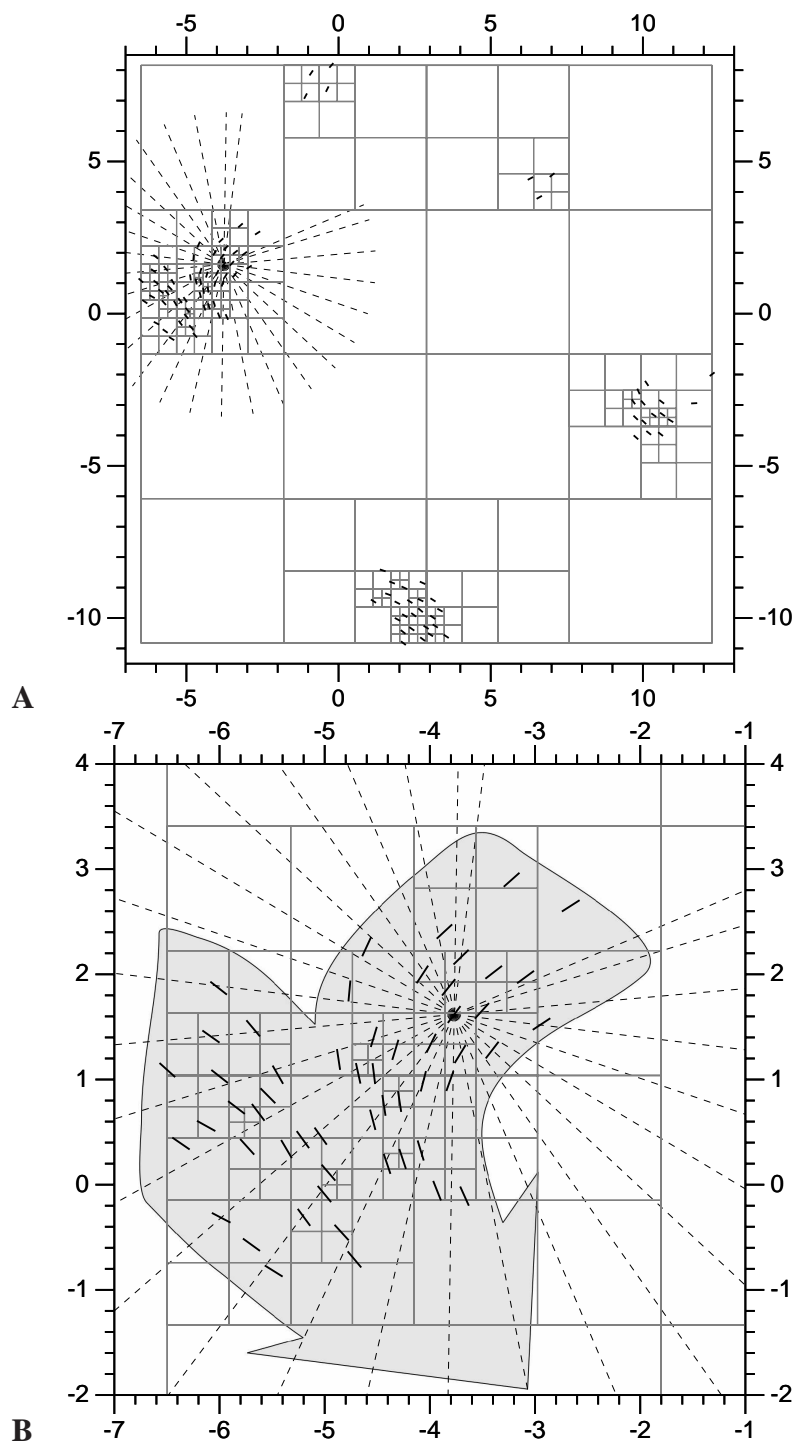


Figure A.1 – Illustration of the hierarchical subdivision of the space into cells (gray squares). **A:** The individuals, represented by short black bars (the center of the line is the reference point) are organized in five groups of different size. The dotted lines illustrate the sensory sectors of a focal individual. **B:** Closer view of the group with the focal individual. Note also the blind area at the back of the individual. Direction of movement is illustrated by the gray arrow.

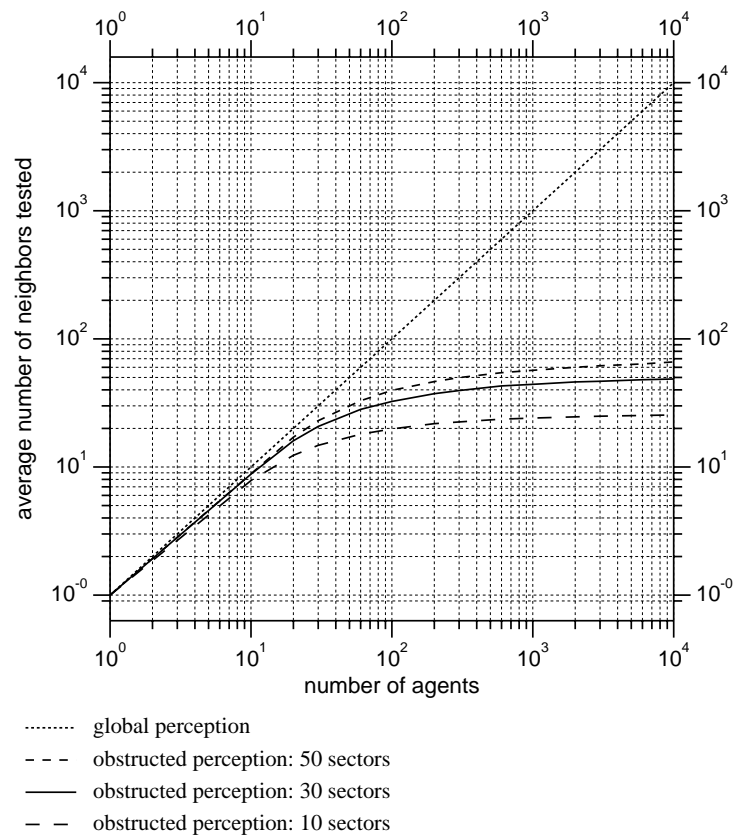


Figure A.2 – Average number of evaluations of neighbors that are required to find the interaction partners per individual per time-step.

always smaller than for the naïve approach. For 10000 individuals the tree-method is more than 200 times more efficient.

Similar algorithms have been developed by Erra et al. (2009); Reynolds (2006); Silva et al. (2008) .

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